

*STUDIES IN
BOTANY*

VOLUME TWO

STUDIES IN BOTANY

A Complete Textbook for
Degree Course (B. Sc.) Students

VOLUME TWO

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To Our Teacher

PROFESSOR HEMENDRA CHANDRA MUKHERJI

this book
is respectfully dedicated

Preface

IN THIS EDITION the subject matter has been carefully and thoroughly revised in order to bring the text up-to-date, but the general plan of the book has not been changed. Cytology, Genetics and Plant breeding sections have been considerably expanded.

We wish to offer our sincer thanks to many of our friends and colleagues for the valuable suggestion they have given us in the preparation of this edition.

CALCUTTA

AUTHORS

Preface to the Second Edition

THE PROSPECT OF A NEW EDITION of any textbook is always a delightful one, because it indicates that the earlier edition has proved acceptable to students, teachers and others interested in this branch of science. In this edition we have endeavoured to bring the text up-to-date and complete for the B. Sc. students through addition of many new facts, illustrations and references. Certain articles have been completely rewritten and a chapter on Biometry has been added to cover the syllabus of the different Universities.

We wish to express our deep sense of gratitude and indebtedness to Sri N. K. Mitra of the Economic Botany Section, State Agricultural Research Institute, Calcutta for his kind help in preparation of the new chapter on Biometry and also for his critical perusal of the entire manuscript for this edition.

We are indebted to the Literary Executor of the late Sir Ronald A. Fisher, F.R.S., to Dr Frank Yates, F.R.S., and to Oliver & Boyd, Edinburgh, for permission to reprint Tables III, IV and VII (in abridged form) from their book *Statistical Tables for Biological, Agricultural and Medical Research*, Sixth Edition, 1963.

Thanks are also due to our colleagues and wellwishers in different Colleges and Universities, specially to Dr Subhendu Mukherji, Department of Botany, Calcutta University; Sri Dilip Gupta and Dr Kalipada Sarkar of the Faculty of Agriculture, Kalyani University; Sri Subodh Roy, Balurghat College (West Dinajpur); Sri N. M. Dutta and Sri Prasad Mukherji, City College, Calcutta; Dr. B. N. Sanyal and Sri S. P. Singha Roy, Anandamohan College, Calcutta; Sri Pijus Roy, Vidyasagar College for Women, Calcutta;

Sri Hrisikesh Chatterjee, Vivekananda College, Barisha, for their constructive suggestions towards the improvement of this edition, and to Sri D. N. Guha Bakshi of the Botanical Survey of India, Calcutta for providing literature and necessary information whenever required by us.

In presenting this volume we have freely consulted a large number of authoritative books and periodicals which have been included in the rather extensive lists of references. Most of the illustrations are from original drawings, but those that have been adapted or redrawn due acknowledgment to the sources has been made in the legends for the figures.

Any suggestion for the improvement of the book will be acknowledged with thanks.

CALCUTTA

D. M.
J. G.
S. K. C.

Preface to the First Edition

THIS volume is meant for B. Sc. (Part II) students of the Indian Universities—it, practically, needs no introduction as the aim and object in writing this book has already been explained in volume one. This text deals with the important field of plant-science, namely Plant Physiology, Ecology, Plant Geography, Economic Botany, Evolution, Cytology, Genetics and Plant Breeding which, we think, will remove the long-felt difficulty for students as well as for teachers. We have consulted freely the old classical as well as recent and up-to-date literature as far as possible and tried to make the text lucid, concise and linkwise so that readers can go through the book easily.

The authors are greatly indebted to Sri Nirmal K. Mitra of the Economic Botany Section, State Agricultural Research Institute, Tollygunge, Calcutta for his valuable help in the preparation of the Plant Physiology and Economic Botany portions.

We are sorry for the lapse of about two years in between the publication of volume one and that of volume two. In spite of our repeated proof-readings we could not avoid some of the printer's devils creeping here and there in the body of the book and which have been corrected under 'errata' at the end. Any suggestions for the improvement of the book will be thankfully acknowledged and as far as possible, followed by the authors.

CALCUTTA

D. M.
J. G.
S. K. C.

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* Thoroughly rewritten and enlarged by Jibes Guha

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PLANT PHYSIOLOGY

CHAPTER I

Chemical Background

A. ATOM—MOLECULE—ELEMENT

1.1 Atom, molecule and element : The *smallest part of an element that can take part in a chemical reaction is known as atom* ; while the *smallest particle of an element or a compound that can exist in the free state* can be defined as a **molecule**.

When a matter is allowed to be divided into smaller particles, a stage would reach when no further division would be possible. These indestructible, indivisible¹ and discrete particles have been designated by John Dalton (1808) as atoms.

An atom is identified by its mass represented by atomic weight and the charge on its nucleus represented by atomic number.

A substance with only one kind of atom and having the same nuclear charge is called an **element**, which cannot be decomposed into simpler substances by ordinary chemical reactions. An element is, therefore, "*the basic chemical type of matter*" whereas an atom is "*the basic physical structure of matter*." Thus gold, silver, lead, copper, mercury, oxygen etc. are elements. If we attempt to analyse the composition of multitudes of living and non-living things present on the earth, these will be found to have derived from the various combinations of just 105 elements (92 naturally occurring and 13 synthetic).

About 97%—98% of earth's crust, ocean and atmosphere is made up of the following eight most common elements—oxygen, silicon, aluminium, iron, calcium, sodium, potassium and magnesium ; whereas the other elements are less abundant.

The most abundant elements in living things are oxygen, hydrogen, nitrogen, carbon, sulphur and phosphorus. Lesser quantities of potassium, calcium, magnesium, sodium, zinc, manganese, cobalt and boron are also present.

1.2 Atomic structure : The main understanding of the fundamental picture of the atom is due to the work of two eminent physicists—Ernest Rutherford of England and Niels Bohr of Denmark. According to them an atom consists of an extremely minute core called the **nucleus** which carries *positively (+) charged protons* (p), *uncharged neutrons* (n) and a *circumnuclear cloud of negatively (–) charged electrons* (e) which are supposed to be revolving about the nucleus in regular and defined closed orbits.

¹ The concept of indivisibility of atom holds good so far as ordinary chemical reactions are concerned ; because atoms can be split in nuclear reactors and other high energy processes.

The number of protons in an atom is equal to the number of neutrons and since the atom as an unit is electrically neutral the extranuclear electrons are numerically equal to the number of protons.

Hydrogen (H) with only one proton and one electron and helium (He) with two protons and two electrons represent the two simplest elements (Fig. 1.1). Thus the hydrogen atom has a nucleus which consists of a simple proton and has no neutron. The single electron orbits around the proton. The electron is moving so rapidly that it would appear everywhere at once, forming a "cloud-like" appearance around the proton.

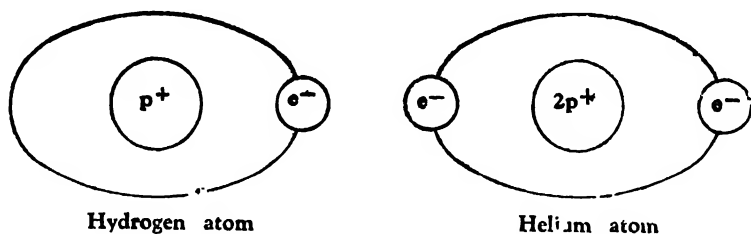


Fig. 1.1

Atoms of the other elements are more complex. Carbon (C) has six protons, six to eight neutrons and six electrons. The most complex of all the elements that occur naturally on earth is uranium (U) which has 92 protons, 140-147 neutrons and 92 electrons.

The modern concept or the wave nature of electron : During the 1920s the researches of De Broglie, Schrodinger, Davisson, Germer, Thomson and others have proved that the electrons also possess wave like properties. When a beam of electrons is directed on to the surface of a nickel crystal and the reflected beam examined by a X-ray spectrometer, the diffraction pattern obtained is similar to the diffraction pattern of X-ray. Thus the electrons may behave both as *material particles* when we consider the velocity and momentum of electrons in a discharge tube and *electro-magnetic waves* when the position of electrons in the diffraction patterns reflected from crystal surfaces are considered. In other words, "electrons behave like a train of waves when passing through space between the atoms of a crystal or through a narrow slit, but when they strike against matter they behave like particles."

1.3 Atomic number and atomic weight : The atomic number of an element is equal to the number of positive charges on the nucleus of an atom which is equal to the number of protons in the nucleus as well as to the number of planetary electrons.

The atomic weight of an element is equal to the sum of the weights of protons and neutrons present in the nucleus. Thus the atomic number of hydrogen is 1, helium 2 and lithium 3 ; whereas the atomic weight of these elements is 1, 4 and 7 respectively.

The atomic weight of an element is the number expressing how many times an atom of the element is heavier than $\frac{1}{16}$ th part of an atom of oxygen or $\frac{1}{12}$ th part

of an atom of carbon⁻¹² and is equal to the ratio of the weight of one atom of the element to $\frac{1}{12}$ th of the weight of one atom of oxygen or $\frac{1}{12}$ th of the weight of one atom of ^{12}C .

A convenient way of representing an element consists of the symbol of that element with a subscript and superscript. The subscript signifies the atomic number of that element whereas the superscript signifies the total number of protons and neutrons (atomic weight). Thus hydrogen, helium, lithium can be represented as $^1\text{H}^1$, $^2\text{He}^4$, $^3\text{Li}^7$ respectively.

1.4 Isotopes : From what has been stated so far it would appear that atoms of an element are identical and have only one number as its atomic weight. But while studying the properties of positive rays with inert non-radioactive neon in the discharge tube, Thomson (1912) demonstrated the presence of two different kinds of atoms of neon with different atomic weights. Soddy (1913) observed similar phenomena with the study of products of disintegration of radio active elements and termed it as isotopy.

The atoms of an element having the same atomic number (number of protons in the nucleus), same chemical properties but different atomic weights (to be specific atomic masses) are called isotopes of that element.

The difference in the atomic masses of various isotopes of an element is due to the number of neutrons in the nucleus, which varies in the different isotopes, but the number of protons is constant for all the isotopes of a given element. Since the electrons determine the chemical properties, the isotopes of an element are identical in all properties including chemical properties but differ in some physical properties e.g. density, rates of diffusion etc. Isotopes are often designated by *mass number* i.e. the total number of protons and neutrons in the nucleus. Carbon has three natural isotopes e.g. ^{12}C , ^{13}C and ^{14}C which may be represented as follows :

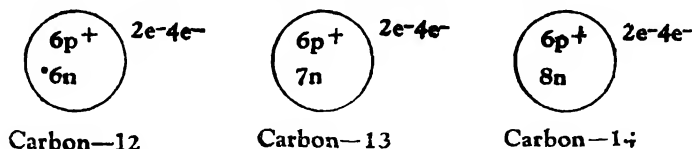


Fig. 1.2 Carbon with its three natural isotopes.

Similarly hydrogen has three isotopes viz., common or light hydrogen, deuterium or heavy hydrogen and tritium, having the mass numbers 1, 2 and 3 respectively. Oxygen has three isotopes of mass numbers 16, 17 and 18.

¹ In order to remove the anomaly in the atomic weight used by the physicists and chemists it was decided in 1961 to accept the isotope of carbon having the mass number of 12 as the standard for atomic weight and was assigned the value of exactly 12.

1.5 Radioactivity : radioactive isotopes : Atoms of most of the elements in nature remain unchanged i.e., they keep their original structure with a fixed number of protons, neutrons and electrons and do not give off light, heat or any other form of energy—these are known as *stable* or *non-radioactive elements*. On the other hand certain atoms keep breaking down, decaying, disintegrating by emitting radiation i.e. shooting out particles and rays and are naturally *unstable* or *radioactive*. The phenomenon of radioactivity is characterised by the emission of (i) alpha rays composed of positively charged α particles, (ii) beta rays composed of negatively charged β particles (electrons) and (iii) gamma rays—electro magnetic energy radiations of very short wave lengths.

In the process, a radioactive atom no longer remains the atom of the original element but becomes atom of another element. When an atom loses an α (alpha) particle, with loss of 2 protons and 2 neutrons, it becomes an atom of another element with an atomic number 2 digits smaller and an atomic weight 4 digits smaller. Thus when an uranium-²³⁸ atom emits an alpha particle, the atomic number is reduced from 92 to 90 and the atomic weight becomes 234 in place of 238 or in other words uranium-²³⁸ atom becomes a thorium-²³⁴ atom. Similarly, radium⁸⁸ (⁸⁸Ra) atom with emission of 3 alpha particles, (loss of 6 protons) becomes an unstable isotope of lead (⁸²Pb), which subsequently by the emission of beta and alpha particles becomes the stable form of lead (⁸²Pb). This transformation of radium to lead i.e. transformation of one element into another is known as *transmutation of the element*.

Natural radioactivity was discovered by Becquerel (1898) in uranium. Mary and Pierre Curie discovered two more radioactive elements—polonium and radium from uranium mineral pitch blende in 1898-99. The discovery of artificial radioactivity goes to the credit of I. Curie and F. Joliot (1934).

Isotopes of element which emit radiation are known as *radio-active isotopes* or *radio-isotopes*. Most elements do not have naturally occurring radioactive isotopes, but the desired isotopes can be produced artificially by bombardment in a cyclotron or nuclear pile.

Half life of radioactive substances : The *half life*¹ of a radioactive isotope is the 'time taken for the activity of a radioactive element to decay to half its original value' i.e., the length of time during which the strength of radiation is reduced to half its original strength. For example, radium (Ra) has a half life of 1590 years, at the end of first 1590 years half of the radium atoms of a given sample disintegrate ;

¹ **Biological half life :** The time required for a biological system to eliminate, by natural processes, half the amount of a substance that has been either produced or absorbed by it.

Effective half life : The time required for the activity of a radioactive substance absorbed in a biological system to lose half its intensity. It is a function of the rate of radioactive decay of the substance and the rate at which the substance is eliminated from the system.

at the end of second 1590 years half of the remaining atoms disintegrate and so on till about 10 half life periods when the radioactivity becomes too weak to be measured. The half life periods of isotopes of even the same element vary considerably e.g. three radioactive isotopes of carbon— ^{10}C , ^{11}C and ^{14}C have the half lives of 9 seconds, 20 minutes and 5740 years respectively.

DETECTION OF RADIOACTIVITY : The emissions from radioactive substances can be detected by various methods *viz.*, (i) Cloud chamber (expansion or diffusion types), (ii) Bubble chamber, (iii) Coincidence counter, (iv) Scintillation counter, (v) Geiger Muller counter or simply Geiger counter and (vi) Photographic methods. Detection of radiation by all these methods is based on phenomena of ionization due to displacement of electrons to higher energy levels.

Of the various methods available for detection of radiations, the Geiger counter method and the photographic method (*autoradiography*) has been put to greatest use in the study of biological systems. Geiger counter is an electronic instrument for direct detection of ionizing radiation from radioactive sources. In the most simplified form, it consists of a metal cylinder or metal lined glass cylinder filled with gas at low pressure. In the centre of the tube there is a positively charged central wire, while the body of the metal cylinder is negatively charged. A high potential is applied between the central wire and the wall of the tube. When a Geiger tube is placed near a radioactive substance, the emitted particles or rays cause ionization of some of the gas molecules in the tube. The ions thus formed create a current that flows from the cylinder to the wire. The current flows out of the tube, through a resistance and then through an amplifier tube to make the impulses strong enough to be heard or seen. One form of the apparatus indicates the presence of radiations by flashes of light, in another the amount of radiation is graphically recorded, while in a third type a clicking sound indicates the presence of radioactivity.

The photographic method is based on the fact that the emissions from radioactive substances affect the emulsion on photographic film or paper, in somewhat the same manner as ordinary light. If a substance containing radioactive material is placed on X-ray plate and exposed for some predetermined time, after developing the plate in the usual way, the presence of radioactivity is observed from the blackening of the plate. The degree or depth of darkening gives a rough measure of the concentration of the radioactive material in different parts of the test substance. The process is known as **autoradiography**.

The emission of particles and rays by radioactive isotopes and the easy methods available for their detection, has rendered possible the use of a very potent tool in the investigation of life processes of plants and animals. The method known as "**tracer technique**" consists of incorporating "**tagged**" or "**labelled**" atoms of either a

radio isotope or an uncommon stable isotope in the molecules of a compound which is allowed to be absorbed by the test organism ; subsequent detection (or tracing) of the isotopes indicates their distribution in the organism and also the reactions in which they participate. For example, when *Chlorella* (a green alga) is allowed to grow in an atmosphere containing $^{14}\text{CO}_2$, the compounds formed in the process of photosynthesis are all labelled with the radioactive isotopes. These compounds can then be extracted from the plant and separated by paper chromatography. An autoradiograph of the chromatogram can be made by placing it on a photographic plate. On developing the plate, the presence of radioactive carbon in different individual compounds is indicated by dark spots. With the refinement of experimental technique it is now possible to identify intermediate metabolites even when they are present in concentration as low as 10^{-6}M in samples weighing only a few milligrams.

"The application of isotopes as tracer for studying the mechanism of chemical reactions and investigating life processes is now regarded as one of the most important advances in the history of chemistry and biology. The outstanding advantage of the isotope technique is that it can be used in studies of normal organisms under normal conditions. It has yielded proof of the truth of some old theories and has completely disproved others. It has provided answers to some problems which could not be solved by previously known experimental techniques. It is at the moment the most promising method of many other problems in physiology and biochemistry which still await solution.

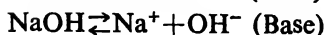
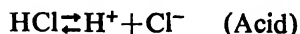
Overexposure to radiation can have serious consequences for living organisms, because ionizing particles can destroy cells. Extreme care is therefore necessary for persons handling radioactive substances to shield themselves from harmful amounts of radiations. However, we are being continuously subjected to weak natural radiations from (a) radium and uranium present in minerals around us (b) bombardment by cosmic rays and (c) radioactive atoms e.g. ^{14}C and ^{40}K present in our bodies."

B. CHEMICAL REACTIONS

1.6 Acids, Bases and Salts : To find a clear understanding of the nature and behavior of matter, scientists from different corners of the world try to classify matter from time to time. Thus in the Middle ages Alchemists recognised two main groups of compounds. The first group is characterised by corrosiveness, sourness of taste and power to turn litmus dye red ; whereas the second group is characterised by brackish taste. It turns indicators a different colour. Members of the first group are called acids, whereas members of the second group are called bases.

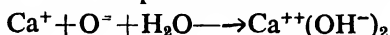
Later, however, the idea has been completely changed and it has been recognised that an acid is a substance which forms hydrogen

inos in solution. A base on the other hand can furnish hydroxide ions.

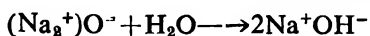


This is known as *ionization*, resulting in the formation of *ions*. Ions are atoms or groups of atoms that are electrically charged. When they carry positive charge, they are called *cations*, and when they carry negative charge are called *anions*. The hydrogen ion (H^+) is called a proton.

Acids and bases can be prepared by the reactions of water with the oxides of the elements. Oxides of the elements on the left hand side of the periodic table help in the formation of bases, i.e.,

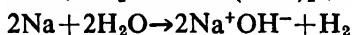
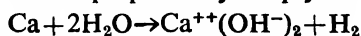


Calcium hydroxide

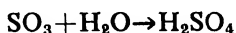


Sodium hydroxide

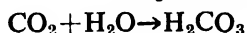
or the same base can be prepared by simply reacting with water.



Acids, on the other hand, can be prepared by the elements of the right hand side of the periodic table by simply reacting with water i.e.

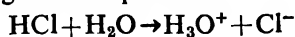


Sulphuric acid



Carbonic acid

There are many acids like HF, HCl, HBr and HI which are derived from halogen derivatives of hydrogen and which, however, do not exhibit any property of acids until and unless they are dissolved in water. Protons from these acids are then transformed to the solvent (water) according to the equation :



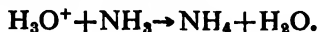
These H_3O^+ ions are taken as *hydronium inos*. For biological purposes we may ignore the hydration of ions and the ionization of water can be represented as



Hydrogen ion Hydroxyl ion

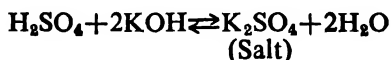
In 1923 Danish chemist Bronsted proposed a new definition for acids and bases. According to him *any molecule or ion that can donate a proton (H^+) to any other molecule or ion is called an acid whereas the molecule or ion when accepts a proton is called a base.*

On the basis of this definition it is clear that ammonia (NH_3), though it has got no hydroxide, is a base. i.e.,



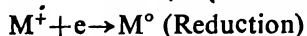
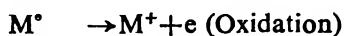
The concentration of the hydronium ions and more simply hydrogen ions determines the degree of acidity of solutions. Similarly the greater the proportion of hydroxyl ions the stronger will be the basicity of solution.

A salt may be defined as a compound resulting from the replacement of one or more of the replaceable hydrogen atoms of an acid by a metal or simply a reaction between an acid and a base results in a salt.



This type of reaction is known to be *neutralization* whereas the reverse reaction is known to be *hydrolysis*.

1.7 Oxidation-reduction : Many of the chemical reactions are energy releasing, whereas others are energy requiring. The chemical changes that release energy are generally known as *oxidation* which means the reaction with oxygen (or hydrogen removed from it), where as the opposite sorts of changes, those which require energy, are known as *reduction*, that is to say, reaction in which oxygen is removed (or hydrogen is added to it). But to-day the definition involves the transfer of electrons. Thus *the loss of electrons by ions or atoms is known as oxidation* whereas *the gain of electrons is known as reduction*.

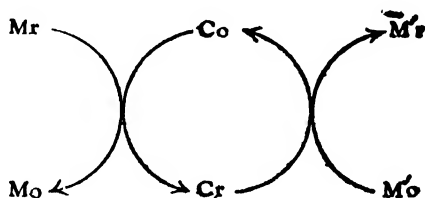


In this type of reaction the oxidising agent gains electrons and is oxidised. This transfer of electrons tends to change the valency of the corresponding atoms or ions, that means the valency of a reduced atoms or ions is decreased. Thus Fe to Fe^{++} , Cl to Cl_2 Cu to Cu^{++} etc. are the cases of oxidation because in all these cases the valency of the atom or ion increases in the following manner. In the first case from O to +2, in the second case -1 to 0 and in the third case 0 to +2.

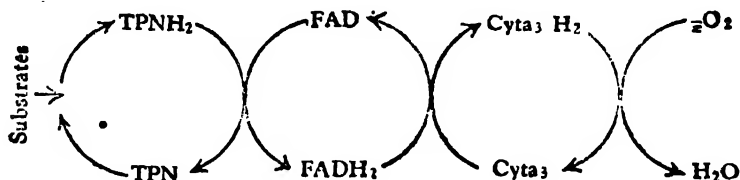
Oxidising and reducing agents may differ among themselves in strength. Strong oxidising agents have pronounced tendency to gain electrons. They are therefore able to remove electrons from many reducing agents (including weak reducing agents which yield electrons with difficulty). Weak oxidising agents on the other hand have a much less pronounced tendency to gain electrons. They can, therefore, oxidise only the strong reducing agents (i.e., which can yield electrons easily). The strength of these oxidising and reducing agents can therefore, be expressed by *oxidation potentials* and more correctly by *oxidation-reduction potentials (redox system)*.

1.8 Biological oxidation : The energy which every cell uses in the performance of work is obtained by oxidation of metabolites with water and carbon dioxide as the chief products. The products are obtained from carbohydrate, fat and protein through a complicated series, of metabolic changes, of which the oxidations are the final steps. The main biological functions of the oxidation and reduction system appear to be the transfer of electrons from metabolites to molecular oxygen.

The most important term in the electron transfer system is the “carriers”—which carry the electron from one substance to another. According to Baldwin (1952) such carrier (C) can react with two different oxidation-reduction systems—M and M'. The oxidised form of carrier (C_o) can oxidise the reduced form of the metabolite (M_r) and the reduced form of carrier (C_r) will be rapidly oxidised by the oxidised form of another metabolite (M'_o). The net effect will be the transfer of electron from M_r to M'_o which has been schematically represented as



The most important electron carriers in biological system are pyridine nucleotide (DPN and TPN), flavin nucleotide (FAD) and metal porphyrins (cytochrome). Ascorbic acid and polyphenols may also serve as electron carrier. It should be noted that the reduced form of the pyridine nucleotide act as a good reductant of the oxidised form of the flavin nucleotide or cytochrome a_3 , but the oxidised form of the pyridine nucleotide would not be reduced by the reduced form of other two systems. Similarly the reduced flavin nucleotide could be oxidised by the oxidised cytochrome but the reduced cytochrome can not be oxidised by the oxidised forms of either flavin nucleotide or pyridine nucleotide. The ultimate electron acceptor is the molecular oxygen and the reduced forms of all three electron carrier systems may react with molecular oxygen. This electron transfer system can be schematically represented by the following diagram.



1.9 Units of standard solutions: Standard solutions are solutions of accurately known concentration. In plant physiology various types of standard solutions are used and the units of these standard solutions are as follows :

(a) **PERCENTAGE CONCENTRATION**—There are different ways for expressing the percentage concentration of a solution. But the most accepted definition is *the number of parts of solute by weight per 100 parts of solution by weight*, which is known as **weight percentage** (or percent by weight or %w/w). For example, a 5% solution of glucose means that each 100 g of solution contain 5 g of glucose and 95 g of distilled water. Similarly a 10% solution of alcohol is prepared by mixing 10 g of alcohol with 90 g of distilled water. But when it is a case of solution of a liquid in liquid it is convenient to express *the percentage by volume* which is known as **volume percentage** (or percent by volume or %v/v) i.e. when 10 ml of alcohol in mixed with 90 ml of water it produces a 10% solution of alcohol.

(b) **MOLARITY**—*When one gram molecule (molecular weight expressed in gram) of a substance is dissolved in water and made up exactly one litre of solution at 20°C, the result is the volume molar or more precisely the molarity (M) of the solution.*

The molecular weight of a substance i.e., the sum of the atomic weights of all the atoms contained in a molecule when expressed in grams is known as the *gram molecular weight* or the *gram molecule* or a *mole*. If the gram molecule of HCl is 36.46 g HNO_3 63.0 g CH_3COOH is 60.05 g etc. and if these amounts are dissolved in water to make a volume upto 1 litre, the solution may be designated as 1M HCl, 1M HNO_3 , 1M CH_3COOH respectively.

A molar solution can be half molar (0.5M), tenth molar (0.1M), fiftieth molar (0.02M) etc. if half, one tenth, one fiftieth of the molecular weight of the substance is dissolved to make exactly 1 litre of solution.

A molar solution can be converted to any strength by diluting with appropriate amount of water. Thus, if a known volume of molar solution be diluted exactly with same amount of water (solvent) it will give a half molar (0.5M) solution. Similarly dilution of a given volume of molar solution with 9 times its volume of solvent will give one-tenth molar (0.1M) solution.

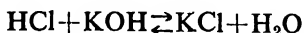
When one mole (gram molecular weight) of a solute is dissolved in 1000 g of the solvent, the solution is called a weight molar or molal solution.

(c) **NORMALITY**—*Normality of a solution is the number of gram equivalents (equivalent weight expressed in grams) of solute per litre or the number of milligram equivalent (equivalent weight expressed in milligram) per litre in a given reaction. It is generally expressed by the letter "N".*

It is clear, therefore, that the concept of normality is closely related to the concept of gram equivalent. The equivalent weight of a substance can be determined as

$$\text{Equivalent weight} = \frac{\text{Molecular weight}}{\text{No. of H or OH per molecule}}$$

Gram equivalent of HCl can be determined by the following equation

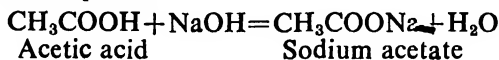


The molecular weight of HCl is 36.46 and since the above reaction yields only one ion of hydrogen the equivalent weight of HCl will be

$$\text{Eq. wt. (HCl)} = \frac{36.46}{1} = 36.46$$

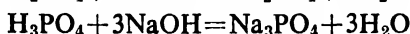
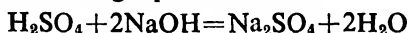
So, 36.46 g of HCl if dissolved in 100 ml of water it will give a normal solution of HCl and should be expressed as 1(N)HCl.

Similarly in the equation



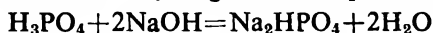
The gram equivalent of CH_3COOH is equal to one gram molecule (60.05g) of CH_3COOH as here also the acid yields one gram ion of hydrogen. In both these cases the normality and molarity is same.

Further the following equations shown :



that two or three hydrogen ions are yielded in the first and second reactions respectively. So the gm. equivalent weight of H_2SO_4 is $\frac{98.08}{2}$ i.e. 49.04 g and H_3PO_4 is $\frac{98.01}{3}$ i.e., 32.67 g

The volume of gram equivalent is not constant but varies according to reactions. As for example, H_3PO_4 yielded hydrogen ions in the previous reactions, but in the following 2 reactions each H_3PO_4 molecule yields 2 and 1 hydrogen ions respectively.



So the gram equivalent in the first reaction is not $\frac{1}{3}$ but $\frac{1}{2}$ of the gram molecule of H_3PO_4 i.e. gram equivalent is $\left(\frac{98.01}{2}\right)$ 49.00 g

whereas in the second case gram equivalent is $\left(\frac{98.01}{1}\right)$ 98.01 g

So according to reactions 32.67 g 49.00 g, or 98.01 g of H_3PO_4 when weighed and dissolved in water to make exactly a litre solution, will give a normal solution of H_3PO_4 .

The normality of a solution can also be expressed as seminormal (0.5N), decinormal (0.1N) and bicentinormal (0.02N) solutions.

1.10 Hydrogen ion concentration: Any aqueous solution, regardless of its chemical reaction contains hydronium (H_3O^+) ions¹ and hydroxyl (OH^-) ions as a result of dissociation of water. Thus



The ionic composition of pure water at 25°C , as determined by measurement of electrical conductivity is as follows.

$$[\text{H}^+] = 1 \times 10^{-7} \text{ moles/litre}$$

$$[\text{OH}^-] = 1 \times 10^{-7} \text{ moles/litre}$$

One litre of water at 25°C contains 55.34 moles of water. So the equilibrium constant for ionization of water (K_i) comes to

$$K_i = \frac{[\text{H}^+] \times [\text{OH}^-]}{[\text{H}_2\text{O}]} \text{ or } \frac{[\text{H}^+] \times [\text{OH}^-]}{55.34}$$

$$\text{Or, } K_i \times 55.34 = [\text{H}^+] \times [\text{OH}^-]$$

Or, $^2K_w = [\text{H}^+] \times [\text{OH}^-]$ (as product of a constant is also a constant) by substituting the values of H^+ and OH^- ion concentration in the above equation, the value of constant K_w comes to

$$\begin{aligned} K_w &= (1 \times 10^{-7}) \times (1 \times 10^{-7}) \\ &= 1 \times 10^{-14} \end{aligned}$$

According to law of electrolytic dissociation, the acidic properties of the solutions depend on hydrogen (H^+) ions and the basic properties on the hydroxyl (OH^-) ions. The concentration of these ions should be equal in all neutral aqueous solutions and in pure water. At 25°C the concentrations are therefore

$$[\text{H}^+] = [\text{OH}^-] = \sqrt{10^{-14}} = 10^{-7} \text{ g moles/litre.}$$

In acid solution the concentration is therefore

$$[\text{H}^+] > [\text{OH}^-] \text{ i.e., } [\text{H}^+] > 1 \times 10^{-7} \text{ and } [\text{OH}^-] < 1 \times 10^{-7}$$

In alkaline solution

$$[\text{OH}^-] > [\text{H}^+] \text{ i.e., } [\text{OH}^-] > 1 \times 10^{-7} \text{ and } [\text{H}^+] < 1 \times 10^{-7}.$$

Since H^+ and OH^- are inversely proportional it is easy to find out the value of any one of them, if we know one of the values. For example, if the hydrogen (H^+) ion concentration of any solution is 10^{-10} gm. ion/litre, the hydroxyl (OH^-) value will be

$$[\text{OH}^-] = \frac{10^{-14}}{[\text{H}^+]} = \frac{10^{-14}}{10^{-10}} = 10^{-4} \text{ g moles/litre}$$

and the solution has alkaline properties.

¹ Hydrogen ion (H^+) never remains free as it is, but it simply unites with water to form a stable ion. Known as *hydronium ion* (H_3O^+). Although it is now accepted that water dissociates into hydronium and hydroxyl ions, in practice, however, the symbol H^+ is used of H_3O^+ .

The constant K_w is called the *ion product of water*.

It is more convenient to express $[H^+]$ and $[OH^-]$ in powers of 10 and to make use of logarithms, thus $0.1N=10^{-1}$, $0.01N=10^{-2}$, $0.001N=10^{-3}$ etc. The exponents -1 , -2 , -3 etc. are the logarithms of the concentrations. Instead of these negative numbers, however, we can make them positive by taking the negative logarithms. *This negative logarithm of the activities of H^+ and OH^- in terms of normality is usually known as hydrogen exponent (pH)¹ and hydroxyl exponent (pOH).*

Thus pH can be simply defined as the negative logarithm of the hydrogen-ion concentration. Therefore acidity is expressed as a power of the reciprocal of the hydrogen-ion concentration. As negative logarithm of a number is the logarithm of its reciprocal, the pH value of the hydrogen-ion concentration of $10^{-3}=3$.

$$[pH = \log \frac{1}{[H^+]} = \log \frac{1}{10^{-3}} = \log 10^3 = 3]$$

In neutral solution $pH=7$, value below 7 on the pH scale represent acid solutions and those above 7, the alkaline solutions.

The relationship between $[H^+]$ and $[OH^-]$ ion-concentration, the pH and pOH values and the nature of reactions of the solutions are given in the following table.

TABLE 1

$[H^+]$	$[OH^-]$	pH	pOH	Reactions
10^0	10^{-14}	0	14	Acidic ↑
10^{-1}	10^{-13}	1	13	
10^{-2}	10^{-12}	2	12	
10^{-3}	10^{-11}	3	11	
10^{-4}	10^{-10}	4	10	
10^{-5}	10^{-9}	5	9	
10^{-6}	10^{-8}	6	8	
10^{-7}	10^{-7}	7	7	Neutral
10^{-8}	10^{-6}	8	6	Alkaline ↑
10^{-9}	10^{-5}	9	5	
10^{-10}	10^{-4}	10	4	
10^{-11}	10^{-3}	11	3	
10^{-12}	10^{-2}	12	2	
10^{-13}	10^{-1}	13	1	
10^{-14}	10^0	14	0	

¹ The expression pH is an abbreviation of French "puissance d' Hydrogen" but the p can also be expressed by terms "potenz" in German and "power" in English used in mathematical sense.

It is evident from the above table that (i) at neutral range both pH and pOH values are 7; (ii) when the pH value is less than 7 it shows an acid reaction and the number diminishes as the acidity increases; (iii) when the pH value is greater than 7 it shows an alkaline reaction and increases with increasing alkalinity; (iv) increase of pH value by one unit corresponds to a tenfold decrease of hydrogen-ion concentration and (v) since a relationship exists between pH and pOH the pH value alone can define the pOH value, so acidity and alkalinity can be expressed in terms of pH units.

If the acidic solution is titrated with an alkaline solution, the hydroxyl (OH^-) ions of the alkaline solution is combined with the hydrogen (H^+) ions and the concentration of the hydrogen ion gradually decreases while the pH of the solution increases. If, however, an alkali is titrated with an acid, the hydroxyl (OH^-) ions are removed by the hydrogen (H^+) ions and the concentration of the hydrogen ions gradually increases and consequently the pH of the solution decreases. At certain definite pH value the equivalence point is reached and the titration must be ended at that point.

DETERMINATION OF pH : The hydrogen exponent or the pH of a solution can be determined experimentally by the following methods :

(i) Potentiometric or E.M.F. method ; (ii) Colorimetric method ; (iii) Freezing point method ; (iv) Catalytic method and (v) Conductivity method.

The basis of the first method is to measure the electromotive force (e.m.f.) of a cell in which the unknown solution is one of the electrode liquids. This e.m.f. is fundamentally connected with hydrogen-ion concentration of the solution (Nernst's equation).

Colorimetric method of pH estimation involves the comparison of the colour of an indicator¹ in the solution of unknown pH with the colour of the same concentration of this indicator in a buffer of known pH .

1.11 Buffers : The term "buffer" is generally applied to solutions which can resist the action of various factors which tend to alter the pH of the solution, consequently it may be compared with the buffer of railway carriages which can resist shocks. If a buffer is introduced in a reacting system, the hydrogen-ion concentration and consequently pH alters slowly despite the formation of an acid or a base in the reaction (Fig. 1.3).

It is clear from A that in the region of abrupt pH change, the curve is almost vertical, which shows that a slight increase of acid or

¹ Indicators are usually complex organic compounds, weak acids or bases, the molecules of which differ in colour from the ions which they form in alkaline or acidic solution. These show one colour if the pH of a solution is below a certain value and a different colour if it is higher.

alkali produces a large change in the pH of the solution. On the otherhand, in B the curve is almost horizontal showing very little change of pH due to addition of acid or alkali. *Solutions which are relatively resistant to change in the pH due to increase or decrease of hydrogen or hydroxyl ions are known as buffer solutions and this type of action is known as buffer action.*

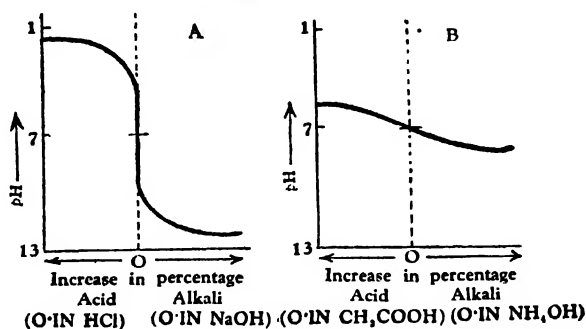
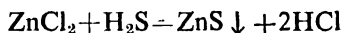


Fig. 1.3 Titration curves.

A—Strong acid with weak base ; B—Weak acid with weak base.

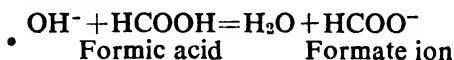
To illustrate this, we may cite the following example. Zinc (Zn) can be precipitated by hydrogen sulphide (H_2S) at pH 2. So, if we want complete precipitation of zinc, we have to use a buffer solution (ammonium formate) of pH 2 to neutralise the solution and then H_2S should be passed through it. Zinc will then be found to precipitate despite the formation of sufficient quantity of acids in the reaction.



The buffer action will be clear from the following facts. Proton (H^+) of the strong acid (HCl) formed in the above reaction reacts with the formate buffer and produces an equivalent amount of the relatively weak acid like formic acid.



and since all the hydrogen (H^+) ions produced react with formate ($HCOO^-$) ions and never remain in a free state, pH of the solution therefore, changes very little. The same type of reaction will follow if we add alkali instead of acid in a solution of formate buffer. The hydroxyl (OH^-) ions of the alkali do not remain in a free state but unite immediately with hydrogen (H^+) ions of the formic acid formed in the above reaction.



So, here also no change of pH takes place.

Titration curve of weak acid and weak base (B) further shows that the addition of acid or alkali will produce a mixture of CH_3COOH and $\text{CH}_3\text{COONH}_4$ which is also a buffer where the changes in the pH takes place very slowly. This is known as acetate buffer. A mixture of acetic acid (weak acid) and sodium acetate (salt) will show buffer action against both acid and base. Similarly the mixture of acid salts of different basicities (*e.g.*, $\text{NaH}_2\text{PO}_4 + \text{Na}_2\text{HPO}_4$) will exhibit buffer action, as here the first salt (NaH_2PO_4) acts as a weak acid and the second (Na_2HPO_4) as its salt.

The basic principle of the buffer action is, therefore, to tie up the hydrogen and the hydroxyl ions produced in the reaction immediately in the formation of compounds which can dissociate very slowly.

PREPARATION OF BUFFER SOLUTIONS: Buffer solution can be prepared in the following way.

0.2M solutions of hydrochloric acid (HCl), sodium hydroxide (NaOH), potassium acid phthalate ($\text{KHC}_8\text{H}_4\text{O}$), potassium dihydrogen phosphate (KH_2PO_4), and boric acid (H_3BO_3)—potassium chloride (KCl) were prepared separately and they were then mixed according to the following proportion. They were then diluted upto 400ml to give rise to the corresponding pH values.

Add 20.40 ml of HCl to 50 ml. of $\text{KHC}_8\text{H}_4\text{O}$ —diluted	to 400 ml to give	...	pH 3.0
Add 0.40 ml of NaOH to 50 ml of $\text{KHC}_8\text{H}_4\text{O}$...	pH 4.0
Add 23.85 ml	pH 5.0
Add 45.40 ml	pH 6.0
Add 29.55 ml of NaOH to 50 ml of KH_2PO_4		...	pH 7.0
Add 4.00 ml of NaOH to 50 ml of H_3BO_3 —KCl		...	pH 8.0
Add 21.40 ml	pH 9.0
Add 43.90 ml	pH 10.0

The above buffer solutions after preparation should be accurately standardised, otherwise a deviation of pH units from the indicated values is expected.

Buffers are now widely used in analytical practices both in qualitative as well as quantitative analysis when the reactions must take place at a definite pH value. The buffer mixtures are also used in the colorimetric determination of pH of solutions.

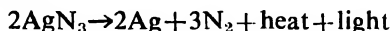
1.12 Chemical energy: Energy may be defined as “the ability to do work.”

There are many situations with which we are familiar where energy is required to get things done. This can be easily illustrated from a power plant near a water fall. The water has the ability to do a work as it drops from the top of the mountain to bottom. As the water trickles down it falls directly on the water wheels placed at the bottom of the falls. The wheel is attached to a generator. The energy released by the falling water would be used

to generate electricity. So the water at the top of the falls has the potentiality for (possibility of) activity. We call this as *potential energy*—the ability to produce *kinetic energy* (energy of motion) as the water drops down on the water wheels.

A substance can yield activity when it changes chemically and is said to contain a special form of potential energy known as **chemical energy**.

Some chemical changes release energy, some require energy. Thus, when silver azide (AgN_3) breaks down into silver atom and molecular nitrogen, a large amount of energy in the form of heat and light is liberated.



Similarly, when methane (CH_4) is allowed to burn in air, a large amount of heat energy is released.



The heat that is liberated can be measured as *calories*¹.

When energy is liberated in the chemical reaction we call it as *exothermic reaction*. If on the other hand, chemical reaction is involved in the absorption of energy we call it as *endothermic reaction*.

The amount of heat released or absorbed in any one of the above reactions can be accurately measured and can be designated by the symbol ΔH . This is said to be the *heat of reaction*.

In case of a chemical reaction, only a part of the energy can be liberated for doing useful work, this is the *free energy* (utilizable energy) of the system and can be designated by ΔF . This free energy system should not be confused with total energy change of a reaction (which is known as heat of reaction, ΔH). Besides free energy, there is an energy which is retained or we may call it as *non-utilizable energy* or *entropy* which can be designated by the symbol S . The more ordered is a chemical reaction, the less entropy there is, and the more random is a chemical reaction, there is more entropy. This non-utilizable energy can be calculated by absolute temperature (T) and ΔS . So a relationship between ΔF and ΔH is given by the expression.

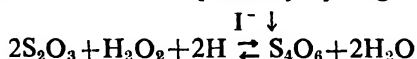
$$\begin{aligned} \Delta H &= \Delta F + T\Delta S \\ \text{Total energy} &= \text{Usable energy} + \text{Non-utilizable energy} \\ \text{Or, } \Delta F &= \Delta H - T\Delta S \\ \text{Usable energy} &= \text{Total energy} - \text{Non-utilizable energy} \end{aligned}$$

That is, once ΔH and ΔS are measured for a chemical reaction, ΔF , the usable energy (free energy) can be readily calculated.

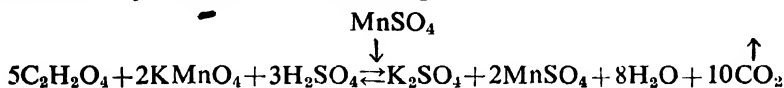
¹ A *calorie (cal)* is a unit of heat. It can be defined as the quantity of heat required to raise the temperature of 1 g of water from 14°C to 15°C. If 1 kilogram of water is used, the heat that will be required will be expressed as "big" *calorie* or *kilocalorie (Cal or Kcal)*.

1.13 Catalyst : *Catalysts are substances which influence reaction rates but are themselves unchanged by the reactions.* The substance is a *positive catalyst* (or *catalyst*) if it speeds up the reaction. The substance that slows down a reaction is called a *negative catalyst* (such catalyst is also known as *inhibitor*). When a product formed in course of a reaction enhances the velocity of the reaction itself is known as *autocatalyst*. Many metals or oxides have catalytic properties.

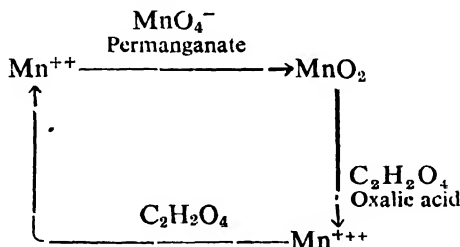
A catalyst may directly be involved in some of the intermediate stages of chemical reactions and which, however, is completely regenerated in the subsequent reactions and therefore is consumed in the reaction. The best example of catalyst is I^- ions which can accelerate the oxidation of thiosulphate by hydrogen peroxide.



Similarly, oxalic acid can be oxidised by permanganate which is accelerated by the addition of $MnSO_4$



It is evident from the above reaction that $MnSO_4$ which is added as catalyst is completely regenerated as one of the products of this reaction. The catalytic action of Mn^{++} ions can be shown as :



A reaction where the catalyst is used to accelerate the reaction and at the same time they are regenerated as one of the products in the reaction is known as *autocatalytic reaction*.

Organic molecules that promote reactions in biological system are called *enzymes*. In living organisms, enzymes act as catalysts accelerating the reaction but without altering the position of equilibrium. (For detail refer Chapter 7).

C. COMPOUNDS OF BIOLOGICAL INTEREST

1.14 Simple organic compounds : In these days of rapid scientific advance, basic sciences play an increasingly important role in the study of biology. We cannot imagine any biological activity which does not involve a biochemical reaction, we must have, there-

fore, a fundamental idea about these bio-organic compounds. The fundamental groups and the structural formulae of some of the compounds of biological interest are given below.

An **organic acid** contains a carboxyl group ($-\text{COOH}$) which can dissociate an hydrogen ion. These are very weak acids and the most common simple organic acid is acetic acid (CH_3COOH).

An **alcohol** contains an alcoholic hydroxyl group ($-\text{OH}$) which, however, does not ionize in the same way as hydroxide ion. The common alcohol is ethyl alcohol ($\text{C}_2\text{H}_5\text{OH}$).

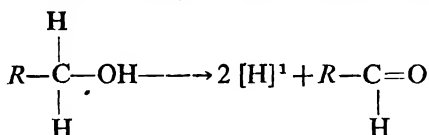
Aldehyde and **ketone** are characterised by a carbonyl group ($\text{C}=\text{O}$). If it is attached by only one other carbon atom $\left(\begin{array}{c} \text{H} \\ \diagup \\ \text{C} \end{array} \right) \text{C}=\text{O}$, it is an aldehyde and if more than one carbon atom is attached $\left(\begin{array}{c} \text{C} \\ \diagup \\ \text{C} \end{array} \right) \text{C}=\text{O}$, it is a ketone.

An **amine** contains an amino group ($-\text{NH}_2$). They are relatives of ammonia.

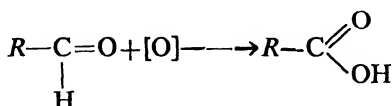
Structural formula	Short form	General name	Common name
$\begin{array}{c} \text{H} \\ \\ \text{R}-\text{C}-\text{H} \\ \\ \text{H} \end{array}$	$\text{R}\cdot\text{CH}_3$	Alkane	Ethane Methane Propane
$\begin{array}{c} \text{H} \\ \\ \text{R}-\text{C}-\text{OH} \\ \\ \text{H} \end{array}$	$\text{R}\cdot\text{CH}_2\text{OH}$	Alcohol	Ethanol Methanol Propanol
$\begin{array}{c} \text{O} \\ // \\ \text{R}-\text{C} \\ \diagdown \\ \text{H} \end{array}$	$\text{R}\cdot\text{CHO}$	Aldehyde	Formaldehyde Acetaldehyde
$\begin{array}{c} \text{O} \\ \\ \text{R}-\text{C}-\text{R}_1 \\ \cdot \end{array}$	$\text{R}\cdot\text{CO}\cdot\text{R}_1$	Ketone	Acetone
$\begin{array}{c} \text{O} \\ // \\ \text{R}-\text{C} \\ \diagdown \\ \text{OH} \end{array}$	$\text{R}\cdot\text{COOH}$	Carboxylic acid	Formic acid Acetic acid

Structural formula	Short form	General name	Common name
$\begin{array}{c} \text{O} \\ \\ \text{R}-\text{C}-\text{O}-\text{R}_1 \end{array}$	R.COO.R_1	Ester	Ethyl acetate
$\begin{array}{c} \text{O} \\ \\ \text{R}-\text{C}-\text{NH}_2 \end{array}$	R.CONH_2	Amide	Acetamide
$\begin{array}{c} \text{H} \\ \\ \text{R}-\text{C}-\text{SH} \end{array}$	$\text{R.CH}_2\text{SH}$	Sulphadryl	Ethanethiol
$\begin{array}{c} \text{H} \\ \\ \text{H} \\ \\ \text{R}-\text{C}-\text{NH}_2 \\ \\ \text{H} \end{array}$	$\text{R.CH}_2\text{NH}_2$	Amine	Ethylamine

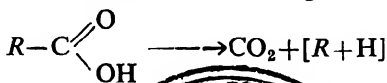
In an alcohol the oxygen atom is attached with a carbon atom and this carbon atom is said to be oxidised. An alcohol can further be oxidised by removing the hydrogen atom from it. Thus by removing two hydrogen atoms aldehyde can be obtained, which is at a higher



level of oxidation than alcohol. By further oxidation this aldehyde can be transformed into an acid which is still at a higher level of oxidation.



This carboxyl group can further be oxidised with the formation of carbon dioxide by removal of the hydrogen atom from it.



The formation of CO_2 is said to be the highest level of oxidation in a biological process.

¹ [-] bracket indicates the unstable or the hypothetical compound and may not exist in the same form as has been shown.

1.15 Complex organic compounds :

A. CARBOHYDRATES: Carbohydrates¹ are compounds which consist only of carbon, hydrogen and oxygen, where the latter two elements are present in the same ratio as in water (i.e. 2 : 1). The empirical formula for carbohydrate is $C_nH_{2n}O_n$ which is identical with the "hydrate of carbon" $C_n(H_2O)_n$ —but this is, however, not true for rhamnose ($C_8H_{18}O_5$), deoxyribose ($C_5H_{10}O_4$), where the proportion of hydrogen to oxygen is not 2 : 1. The most important examples of carbohydrate are sugar, starch, cellulose etc.

The carbohydrates are broadly classified as monosaccharides, disaccharides and polysaccharides.

(i) *Monosaccharides* : It is the simple sugar with only one unit and from which no simpler carbohydrate can be produced on hydrolysis. Monosaccharides can be classified on the basis of number of carbon atoms present.

Monosaccharides Or Simple sugars	{	Dioses (2 - C.c.) ² - $C_2H_4O_2$ e.g.—glycollic aldehyde
		Trioses (3 - C.c.) - $C_3H_6O_3$ e.g.—glyceraldehyde, dihydroxyacetone
		Tetroses (4 - C.c.) - $C_4H_8O_4$ e.g. - erythrose
		Pentoses (5 - C.c.) - $C_5H_{10}O_5$ e.g.—ribulose, xylulose
		Hexoses (6 - C.c.) - $C_6H_{12}O_6$ e.g.—glucose, galactose, fructose
		Heptoses (7 - C.c.) - $C_7H_{14}O_7$ e.g.—sedoheptulose etc.

Monosaccharides can also be classified as aldoses and ketoses based on the presence of aldehyde ($-CHO$) and ketone ($-CO$) group in the molecule. The presence of these groups in a molecule results in the reducing properties of the monosaccharides. This reducing action can be determined by the Fehling's or Benedict's solution, where this sugar converts cupric hydroxide $[Cu(OH)_2]$ to cuprous oxide (Cu_2O). This cuprous oxide settles down as a red precipitate on heating. Monosaccharides are therefore called *reducing sugars*.

Of all the different types of monosaccharides, pentoses ($C_5H_{10}O_5$) and hexoses ($C_6H_{12}O_6$) occur most abundantly in plants. Among pentoses *ribose* is an important constituent of ribonucleic acid (RNA) and of co-enzymes I and II (refer article 7.12). It appears to produce a phosphate ester (ribulose diphosphate) which probably acts as an acceptor of CO_2 in photosynthesis. Deoxyribose occurs in deoxyribose nucleic acid (DNA). *Arabinose* and *xylose* are the other common pentose sugars which are used in the synthesis of other complex molecules.

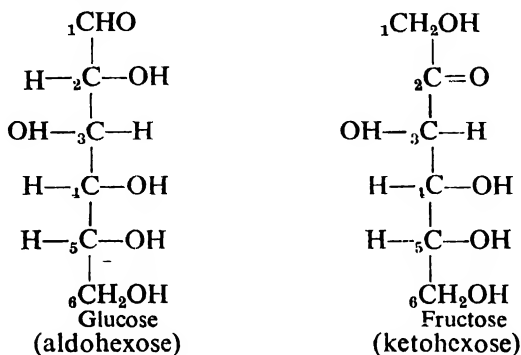
The most common hexose sugars which occur in plants are *glucose* (so called *dextrose*) and *fructose* (so called *levulose*). The chemical formula is exactly the same in both the cases i.e. $C_6H_{12}O_6$ (such substances which have same molecular formula but different chemical

¹ Carbohydrate may also be defined as a "large group of compounds which either are themselves polyhydroxy aldehydes or ketones or closely related compounds or yield such compounds on acid hydrolysis."

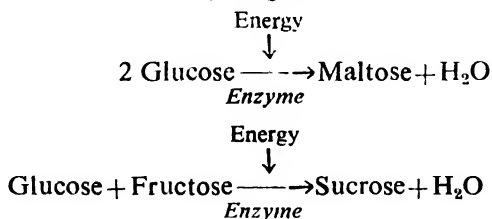
² 2-C.c. means 2-Carbon compound.

properties are called *isomers*), but the former is said to be aldohexose (as it contains an aldehyde group) whereas the latter a ketohexose (as it contains a ketone group). Glucose is dextrorotatory¹ whereas fructose is laevorotatory¹ (which is designated by *d*- or *l*- in the prefix).

The structural formula for glucose and fructose may be shown as follows (the number in the prefix of carbon atom represents the position of carbon atom in the molecule) :



(ii) *Disaccharides* : Disaccharides are formed by the condensation of either two identical molecules of the same monosaccharide or of two different monosaccharides resulting from the elimination of a molecule of water. As for example, *maltose* ($\text{C}_{12}\text{H}_{22}\text{O}_{11}$) is produced by the condensation of two identical monosaccharides (i.e. glucose) and *sucrose* ($\text{C}_{12}\text{H}_{22}\text{O}_{11}$) is produced by the condensation of two different monosaccharides (i.e., glucose and fructose).

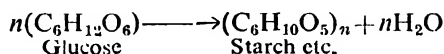


The linking of the monosaccharides in these cases occurs in such a manner that the identity of the aldehyde or ketone groups of the individual monosaccharides is lost. So they do not exhibit any positive reaction with Fehling's or Benedict's solutions. Disaccharides are, therefore, called *non-reducing sugars*. Maltose, however, exhibits reducing property, as during linkage one aldehyde group remains free.

¹ It is the capacity of the substance to change the direction of the polarised light to the left or to the right. If the polarised light is rotated to the right (clockwise) the compound is said to be *dextrorotatory* (*d* or +), if however, it is rotated to the left (anti-clockwise) it is known as *laevorotatory* (*l* or -).

Of all the disaccharides *sucrose* is widely distributed in plant tissues and it accumulates in the storage organs of the plant.

(iii) *Polysaccharides* : Polysaccharides are the complex carbohydrates which are formed by the condensation of a large number of monosaccharides. The ratio of atoms in a polysaccharide is slightly different from the ratio in the simple sugars from which the polysaccharide is derived ; because the valence bonds necessary to link two monosaccharide units together can no longer be attached to the hydrogen atom and hydroxyl radical as in a simple sugar molecule. Some polysaccharides are formed by the condensation of one kind of sugar, whereas others are produced by the condensation of two or more types of sugars. Thus *starch*, *glycogen*, *cellulose*, *inulin* etc. are the examples of former, whereas *gums* and *mucilage* are the examples of latter type. The general empirical formula for polysaccharides is $(C_6H_{10}O_5)_n$ which is found to have derived from hexose sugar.



Starch is abundant in the vegetative tissues particularly in the storage organs of the plant. It also accumulates temporarily in the leaves of many species of plants during photosynthesis.

Each starch molecule is believed to comprise soluble amylose and less soluble amylopectin. Both the components of starch are found to be derived from glucose. Glucose is, therefore, considered to be the starting point of starch synthesis, which is incidentally controlled by two enzymes—P-enzyme and Q-enzyme. Glucose is first converted to glucose-1-phosphate by the *phosphorylation enzyme*. From here it proceeds along two different pathways. In the first, glucose-1-phosphate is converted to amylose by the P-enzyme and in the second it is converted to amylopectin by Q-enzyme which are then combined to form starch according to the following scheme.

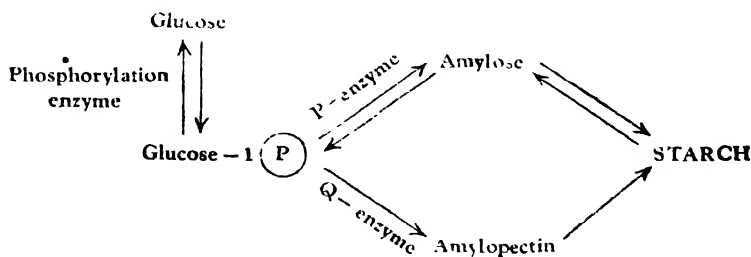


Fig. 1.4 Schematic representation of formation of starch.

Starch is involved in cell metabolism and is the form in which carbohydrate is stored in plants. It forms a blue coloured complex with iodine. This is due to reaction of iodine and amylose. Iodine

and amylopectin form a deep purple colouration. Starch can be hydrolysed to glucose through dextrins and maltose.

Starch→Dextrins→Maltose→Glucose

The most abundant polysaccharide is cellulose—which is an important constituent of plant cell walls. Cellulose forms an important constituent of cotton fibre. Cellulose can be acetylated, methylated and nitrated to give compounds of great industrial importance.

Chemically cellulose is very inert being insoluble in water and in organic solvents. The ultimate products of its hydrolysis is glucose but it is not easy to hydrolyse cellulose.

Nothing is known about the synthesis of cellulose in plants.

Starch and cellulose are known as *hexosans* as they are derived from hexose monosaccharides. Those which are derived from pentoses are known as *pentosans*.

Tests for carbohydrates :

(a) GLUCOSE-FRUCTOSE

(i) *Fehling's test*—Equal volume of Fehling's solution no. I¹ and II² was mixed together and added to a small quantity of glucose solution and then boiled. An orange red precipitate of cuprous oxide (Cu_2O) was obtained. The positive behaviour of the sugars in this test clearly proves the reducing nature of the sugars (e.g. glucose, fructose, etc.).

(ii) *Barfoed's test*—Equal volume of Barfoed's reagent (9 g of neutral crystalloid copper acetate in 100 ml of water and add 1.2 ml of 50% acetic acid) is added to the same volume of sugar solution and then boiled for a few minutes. Red granules of cuprous oxide on the walls of the test tube indicate the reducing properties of sugar solution.

(iii) *Osazone test*—To a sugar solution in a test tube, a few crystals of phenyl hydrazine hydrochloride and twice the amount of solid sodium acetate, then a few drops of glacial acetic acid is added. Kept the test tube in a beaker of boiling water, cooled the test tube and observed the crystalline ppt. (*osazones*) under the microscope. Glucose, fructose etc. produced identical needle shaped osazones.

(iv) *Moore's test*—A portion of sugar solution was heated with half the volume of NaOH, cooled and then a few drops of conc. H_2SO_4 is added. Yellowish brown colouration and a smell of burnt sugar appears proving the reducing properties of sugars.

(v) *Silver mirror test*—To an aqueous solution of sugar in a test tube ammoniacal AgNO_3 is added and boiled the test tube in a water bath. A silver mirror was produced due to precipitation of silver.

(vi) *Seliwanoff's test*—To an aqueous solution of sugar an excess of Seliwanoff's reagent (0.05 g of resorcinol in 100 ml of dil. HCl) is added and boiled. A red ppt. was formed. It is a specific test for ketohexoses (e.g. fructose).

(b) SUCROSE

All the previous tests for reducing sugars will prove *negative* for sucrose.

A little sucrose solution is boiled with a few drops of normal HCl for about 10 minutes. After cooling, the solution is neutralised with normal NaOH. This solution now exhibits all the previous tests for glucose and fructose.

¹ 7 g CuSO_4 dissolved in 100 ml distilled water.

² 25 g KOH, 34 g sodium potassium tartarate dissolved in 100 ml distilled water.

(c) STARCH

(i) *Iodine test*—to a starch solution a few drops of iodine solution is added. The solution turned blue indicating the presence of starch. On heating the solution, the colour discharged and which, however, reappeared on cooling.

(ii) *Tanic acid test*—To a starch solution an excess of tanic acid is added and heated. A white ppt. is obtained and which is dissolved on heating.

B. FATS : Like carbohydrates, fats are compounds of carbon, hydrogen and oxygen but the ratio of hydrogen to oxygen is not 2 : 1.

The term “oils” is usually applied to fats which are liquid at normal temperature (10° – 20°C) and which are chemically same as fats.

Fats are compounds principally of esters of alcohol (glycerol) and various carboxylic acids (fatty acids). Glycerol is a 3-carbon molecule found to have derived from sugars.

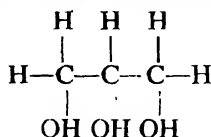


Fig. 1.5 Structural formula of glycerol.

A fatty acid is an organic acid consisting of a long hydrocarbon chain with a carboxyl group at one end and since an organic acid is represented by $-\text{COOH}$ radical, the fatty acid can be represented by the general formula $R-\text{COOH}$, where R stands for the rest of the molecule.

The $-\text{COOH}$ radical of a fatty acid now reacts with the $-\text{OH}$ radical of the glycerol molecule according to the following scheme :

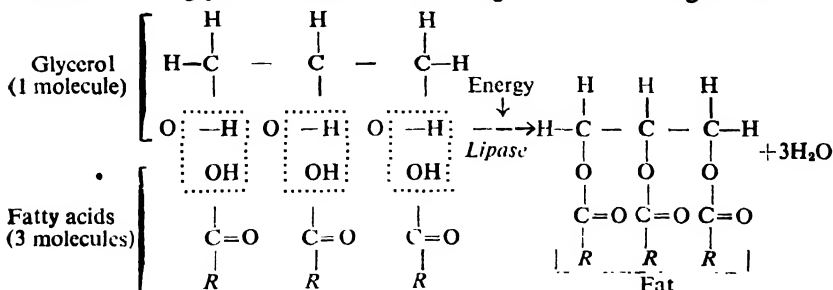


Fig. 1.6 Formation of a fat.

It is evident, therefore, that three molecules of fatty acids (identical or different) must unite with a molecule of glycerol to give rise to a molecule of fat. Three molecules of water being split off in the reaction.

Fatty acids can be either ‘saturated’ when their hydrocarbon chain contains only single bonds or ‘unsaturated’ when one or more double bonds are present.

The important saturated fatty acids in plants are *palmitic acid* ($\text{CH}_3(\text{CH}_2)_{14}\text{COOH}$) found in palm oil, *stearic acid* ($\text{CH}_3(\text{CH}_2)_{16}\text{COOH}$) found in animal and plant fats, and *caproic acid* ($\text{CO}_3(\text{CH}_2)_4\text{COOH}$) found in coconut oil etc, *oleic acid* ($\text{CH}_3(\text{CH}_2)_7\text{CH}=\text{CH}(\text{CH}_2)_7\text{COOH}$) found in olive oil is a typical unsaturated fatty acid.

A number of substances are chemically related to fats. All of which are found to have derived from fatty acids but not in combination with glycerol. All the substances that are built from fatty acids are grouped together and called **lipids**. The most important lipoidal substances are *waxes*, *cutin* and *suberin*.

Tests for fats :

(i) *Hydrolysis of fats (saponification)*—To a small amount of olive oil an excess of 10% NaOH is added in a water bath. Boiled and after cooling Na_2SO_4 is added. The soap formed separates out. It is filtered, the filtrate neutralised with H_2SO_4 . It is evaporated and the residue is dissolved with alcohol. A syrup like liquid is formed which on tests proves to be glycerine.

C. PROTEINS : The proteins are complex nitrogenous organic polymers with high molecular weight. They are the most important chemical constituents of living organisms. The main building blocks of the protein molecules are the **amino acids**. An amino acid is an organic acid which contains at least one amino group ($-\text{NH}_2$) in addition to its usual carboxyl group ($-\text{COOH}$).

Amino acid can be obtained by the replacement of hydrogen of the alkyl (hydrocarbon) radical in a fatty acid by an amino group ($-\text{NH}_2$). The simplest amino acid is *glycine* (Fig. 1.7) which can be

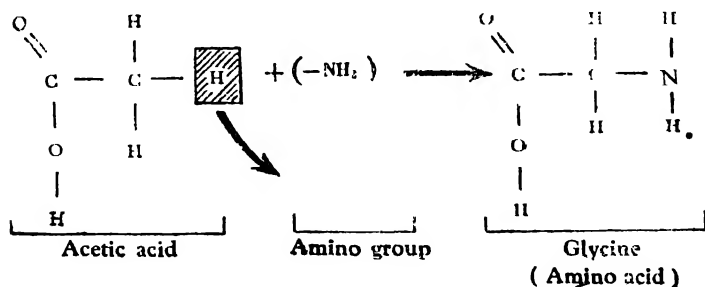


Fig. 1.7 Formation of simplest amino acid (glycine).

obtained from acetic acid (simple fatty acid) by replacing hydrogen atom with an amino-group. Glycine, therefore, contains carbon, hydrogen, oxygen and nitrogen. The other amino acids are more complex containing sulphur, phosphorus and even iodine or bromine in addition to C, H, O and N. If *R* represents the variable number

of amino acids the structure of amino acid can be schematically represented as :

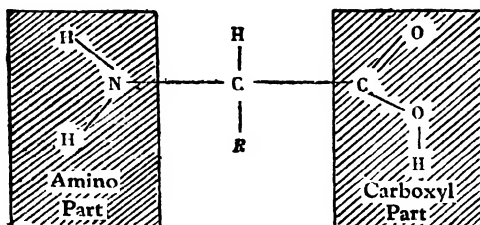


Fig. 1.8 Basic structure of an amino acid. *R* represents a single hydrogen atom; in glycine; in other amino acids *R* stands for several atoms of different kinds.

Proteins are formed by the condensation of amino acids by *peptide linkage*. A peptide linkage is a reaction between the amino group of one amino acid with the carboxyl group of other amino acid—one molecule of water being split off in the reaction. The resulting molecule is called a *dipeptide*. Further condensation of this chain reaction proceeds to produce *polypeptide*, *peptones*, *proteoses* and ultimately to protein.

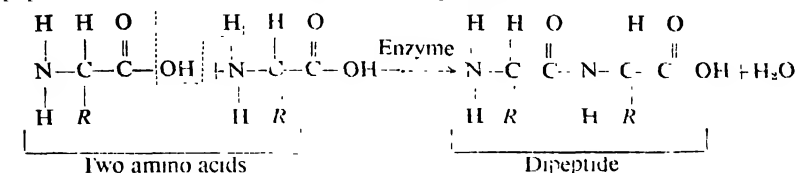


Fig. 1.9 Formation of a dipeptide.

The most commonly occurring amino acids in plants are *tryptophan*, *tyrosine*, *histidine*, *aspartic acid* etc. Approximately twenty different amino acids occurring in plants recombine to produce the enormous number of protein molecules and the synthesis of these proteins is a matter of linking the amino acids together.

The following are the twenty commonly occurring amino acids :

Glycine	Nonpolar	Lysine	Amine bases
Alanine		Arginine	
Leucine		Histidine	
Isoleucine			
Valine			
Serine	Alcoholic	Asparagine	Amides
Threonine		Glutamine	
Tyrosine			
Phenylalanine	Aromatic	Cysteine	Sulphur containing
Tryptophan		Methionine	
Aspartic acid	Carboxylic acids	Proline—Imino	
Glutamic acid			

Based on the physical and chemical characteristics, the protein may be grouped into—

(a) *Simple protein* : Which on hydrolysis yields only amino acids as the sole organic product. *Globulin, albumin, histones* are the examples of simple protein.

(b) *Conjugated protein* : Which contain a number of other organic constituents such as nucleic acid, phosphorus, carbohydrates etc. in addition to amino acids. This non-amino acid portion of the protein is known as the “prosthetic group”. *Nucleoprotein, chromoproteins* and *glucoproteins* are the examples of conjugated protein.

(c) *Derived protein* : Which represents the degradation products of natural proteins. This degradation products are usually *proteoses, peptones, peptides* etc. and they are the examples of derived protein.

Tests for proteins :

(i) *Coagulation test*—When protein solution acidified with acetic acid is heated, coagulation takes place. It is, however, not a very delicate test for proteins—since a trace of protein cannot be detected.

(ii) *Xanthoproteic reaction*—To a protein solution, if a few drops of conc. HNO_3 are added, a white ppt. is produced and which on heating turns yellow. Now adding sufficient ammonia to make the solution alkaline, the colour changes to orange. This test is specific to proteins which contain amino acids like tyrosine, tryptophan and phenylalanine.

The yellow stain produced on the skin when conc. HNO_3 comes in its contact is due to this type of reaction.

(iii) *Biuret reaction*—A drop or two of a dilute solution (1%) of CuSO_4 and excess of strong (4%–5%) NaOH , gives to most proteins a violet colouration. This type of reaction is also exhibited by *biuret*—a substance formed by heating solid urea, ammonia being liberated. Almost all proteins and many of its decomposition products respond to this test, but dipeptide and free amino acid do not.

(iv) *Millon's reaction*—With a few drops of Millon's reagent (a mixture of mercuric and mercurous nitrates with excess of conc. HNO_3) all proteins having a phenolic grouping (e.g. tyrosine) give brick red colouration on boiling. This test is specific for phenol group and not for gelatin.

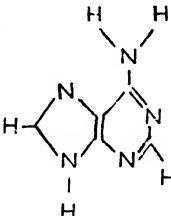
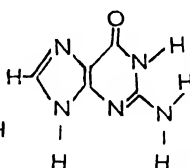
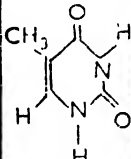
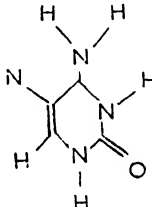
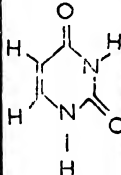
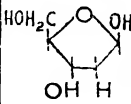
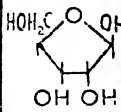
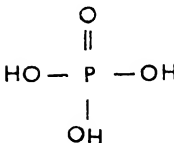
(v) *Molisch's reaction*—To a protein solution, an alcoholic solution of thymol and then strong H_2SO_4 is carefully poured down the side of the test tube. A distinct purple ring is formed at the junction of the two liquids. This reaction is specific to proteins containing carbohydrate radical and the reaction is due to the formation of *furfural* from the carbohydrate with the thymol.

(vi) *Rosenheim's formaldehyde reaction*—When a solution of protein is mixed with dilute formaldehyde and conc. H_2SO_4 is added, a purple-violet ring is developed in the surface of contact. This test is specific for proteins containing tryptophan.

D. NUCLEIC ACID AND NUCLEOTIDE : While studying the chemical constituents of the cell nuclei, Miescher in 1869 obtained an acidic non-protein material which contained an appreciable quantity of phosphorus. He designated this material as “*nuclein*”. This term was, however, replaced by *nucleic acid* in the year 1889 by Altmann.

The first detailed work regarding the chemical composition of the nucleic acids have been made by Jones (1920) in his trinucleotide

hypothesis and Levene (1931) in his tetranucleotide hypothesis. The modern era of structural determination was initiated by the research of Chargaff *et al*; by the development of methods of synthesis of nucleosides, nucleotides and polynucleotides (Todd *et al*, 1951-52; Khorana, 1961) and finally by x-ray and physico-chemical studies of

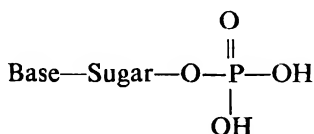
	DNA Only	DNA and RNA	RNA Only
PURINES NITROGENOUS BASE		 <p>ADENINE</p>	 <p>GUANINE</p>
	 <p>THYMINE</p>	 <p>CYTOSINE</p>	 <p>URACIL</p>
PENTOSE	 <p>DEOXYRIBOSE</p>		 <p>RIBOSE</p>
PHOSPHATE			

nucleic acids and their successful interpretation by Wilkins, Watson, Crick and others. A nucleic acid consists of a 5-carbon sugar—ribose or deoxyribose, nitrogenous bases—purines and pyrimidines and phosphates.

The two most important nucleic acids that have been observed from many biological sources are *ribonucleic acid* (abbreviated as RNA) and *deoxyribonucleic acid* (abbreviated as DNA).

In addition to their differences in sugar composition, RNA and DNA also differ in their nitrogenous bases. Thus in RNA the bases are adenine, uracil, guanine and cytosine. In DNA it contains adenine, thymine, guanine and cytosine. In some DNA, however, 5-methylcytosine replaces the position of cytosine.

If one of these purines or pyrimidines becomes attached to a sugar (ribose or deoxyribose) and the sugar is attached to a phosphoric acid they will give rise to a molecule called *nucleotide*. The arrangement of the three components takes place according to the following scheme :



Although the chemical composition of DNA has been investigated as early as 1900, but the arrangement of all these constituents was not possible until 1953 when J. D. Watson and F.H.C. Crick proposed a new model for the structure of DNA. According to them it consists of two strands twisted about one another to form a *double helix* where the chain of each helix bounded by sugar-phosphate groups and the two helices are connected by the hydrogen-bonded bases. One helix is just the opposite to the other and during the synthesis of DNA one helix acts as template for the formation of complementary helix. Structurally RNA differs from DNA. In most cases RNA is a single strand with some twisting here and there.

The structural formula of nucleotide is given in the following diagram.

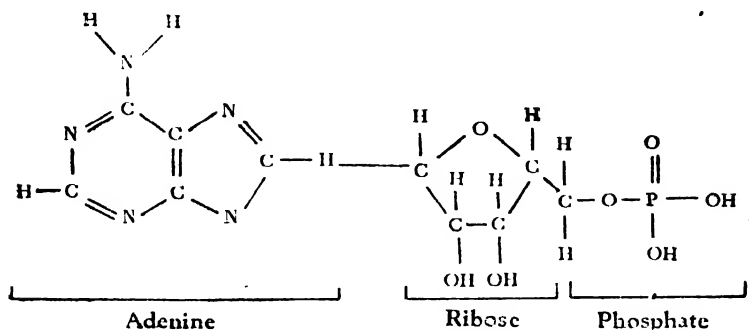


Fig. 1.10 Structural formula of a nucleotide.

The nucleic acids are the most important group of substances in the nucleus as well as in the cytoplasm. DNA is present only in the nucleus and always associated with the chromosomes and is, therefore, important in transmitting information from nucleus to the cytoplasm, whereas the cytoplasmic nucleic acid comprising mainly of RNA is responsible for the protein synthesis.

SELECTED QUESTIONS

1. What do you mean by an atom, a molecule and an element ? What are the elements abundant in living objects ?

Refer article 1.1

2. What is the structure of an atom ? Describe the modern concept of an atom.

Refer article 1.2

3. Distinguish between the atomic number and the atomic weight of an element. How can they be represented ?

Refer article 1.3

4. Define an isotope. What are the important natural isotopes of carbon, hydrogen and oxygen ?

Refer article 1.4

5. Define radioactivity. What do you mean by half-life of radioactive substances ?

Refer article 1.5

6. What are the possible ways of determining radioactivity in plants ? What do you mean by autoradiography ?

Refer topic *detection of radioactivity* in article 1.5

7. What do you mean by "tracer technique" ? How can it be applied in elucidating plant physiological problems ?

Refer topic *detection of radioactivity* in article 1.5

8. How do oxidation-reduction reaction differ from exchange reaction ? What are the roles of the oxidising-reducing agents in biological system ?

For first part refer article 1.7 and for second part of the question refer article 1.8

9. What is the molarity of the solution ? How can it be distinguished from molal solution ? Prepare a molar solution of glucose, sodium chloride and sucrose. Prepare molal solutions of the same compounds.

For first and second part of the question refer article 1.9 (b). For the last part add.

Since the molecular weight of glucose ($C_6H_{12}O_6$) is the sum of the atomic weights of all the atoms in the molecule, the gram molecular weight of glucose is 180. So 180 gms. when dissolved in a litre of water it will give a molar solution of glucose.

Similarly gram molecular weights of sodium chloride (NaCl) and sucrose ($C_{12}H_{22}O_{11}$) are 57 and 342 respectively. When these amounts are dissolved separately in litre of water it will give a molar solution of sodium chloride and sucrose respectively.

The molal solutions of these substances can be prepared by dissolving the above amounts in 1000 gms. of water.

10. Define the terms gram-equivalent, milligram-equivalent and normality of a solution.

Refer article 1.9(c)

11. What do you mean by hydrogen-ion concentration? How can it be determined?

Refer article 1.10

12. Describe the importance of buffer in a chemical reaction? How are the buffer solutions prepared?

Refer article 1.11

13. Write a short account of the carbohydrates giving their classification.

Refer article 1.15A

14. By what chemical tests would you distinguish an aldohexose from a ketohexose.

Refer topic *tests for carbohydrates (a) Glucose-Fructose* in article 1.15A

15. What are the principal disaccharides that you have studied? Mention the products formed when each of them is hydrolysed. Mention some of the important tests for sucrose.

For first part refer article 1.15A (ii)

For last part refer topic *tests for carbohydrates (b) Sucrose* in article 1.15A

16. What is the chemical nature of a fat? How does it differ from an oil? Describe the important tests for fats.

Refer article 1.15 B

17. What are proteins? Name some of the common proteins you know. Mention, with examples, the groups into which proteins have been classified.

Refer article 1.15 C

18. Discuss the results obtained by the hydrolysis of proteins. By what specific reactions are they detected.

Refer article 1.15C. For last part refer topic *tests for proteins*.

19. What are nucleic acids? Describe the role of nucleic acids in plants.

Refer *nucleic acid and nucleotide* in article 1.15D

20. What are isotopes? Discuss briefly the use of isotopes in the study of physiological processes in plants.

Refer articles 1.4 and 1.5

Physico-chemical Properties of Colloidal Systems

2.1 Definition of colloid : Thomas Graham (1860) while studying the molecular size of proteins showed that there are many substances which have a slow rate of diffusion or which failed to diffuse through parchment membrane. He applied to this amorphous non-diffusible substance the term **colloids** (Greek *colla* means glue). The substances have the molecular size 10^{-5} cm to 10^{-7} cm (or $0.001\mu^1 - 0.1\mu$) and are dispersed in a continuous dispersion medium.

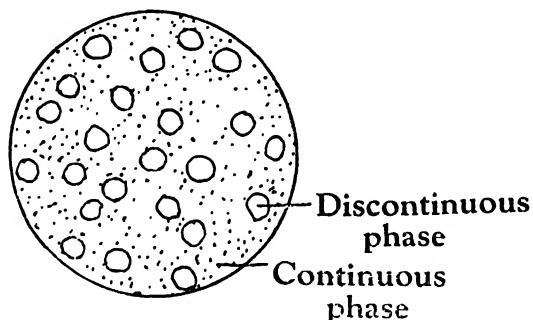


Fig. 2.1 Diagram showing two phases of colloidal system.

The colloidal systems have two distinct phases—a *continuous phase* or dispersion medium and a *discontinuous phase* or the disperse phase (Fig. 2.1). The liquid on which the solid particles are dispersed is a continuous phase and the particles themselves are in a discontinuous phase.

Thus, a substance is said to be in the colloidal state, when it is dispersed in another medium in the form of particles, having diameter between 10^{-5} cm and 10^{-7} cm. These particles form the *disperse phase* and the medium in which these particles are present is called the *dispersion medium*. The whole system consisting of the disperse phase and the dispersion medium is called the **colloidal system** or colloidal dispersion.

2.2 Colloids and crystalloids : Just reverse of colloids there is another group of crystalline substances which, when in solution,

¹ μ stands for micron and is $1/1000$ mm

readily diffuses through a parchment membrane. Graham accordingly applied to these diffusible substances the term *crystalloids* (or true solution). Generally crystalloids have molecular dimensions less than $1m\mu$. That is why the solute particles of crystalloid dispersion can easily pass through the pores of clay or porcelain filters or collodion thimbles, whereas the solute particles of colloidal dispersion cannot. So according to Ostwald (1919) colloidal and crystalloidal particles can not only be separated by *dialysis* but also by *ultrafiltration*.

The crystalloid solutions are in a molecular or ionic dispersed state whereas the colloid solution are physically heterogeneous.

Scattering of light by crystalloids is slight but in case of colloids this scattering of light is quite marked.

A surface tension exists between colloidal particles and the dispersing medium. As a result of this, colloids often show high resistance to flow or in some cases they fail to flow. But crystalloids have no such activity.

Because of their larger size colloidal particles diffuse slowly throughout a solution compared with the crystalloid.

The dimension of the colloidal particles is too small to settle down to the bottom but at the same time too large to form true solution. That is why these lie between solution proper (true solution) and crude suspension. But still the limits are vague and materials can be prepared in colloidal form if the size of the particles falls within the range of 0.001μ — 0.1μ (e.g. many metals like copper, gold, platinum etc.). Substances like sodium chloride can produce a true solution with water and a colloidal solution with benzene. It is, therefore, important to conclude that the *colloid is a particular state of matter and not a particular class of matter*.

It is evident, therefore, that Graham's intention of dividing substances into colloids and crystalloids is not valid, as any substance can be made into a colloidal state by proper physical methods.

2.2 Nature and types of colloidal systems : Colloidal solutions can be divided into two main groups (i) *hydrophobic* (water dreaders) or *lyophobic* and (ii) *hydrophilic* (water lovers) or *lyophilic* system. The term hydrophobe generally applies to the case when the dispersed particles possess but little or no affinity for water. A colloidal system with solid disperse phase (less than $100m\mu$ but greater than $1m\mu$ in diameter) and a liquid continuous phase is called a *suspension*. A suspension generally belongs to the former group. Clay in water, sulphur in water etc. are the examples of suspension. A suspension is very unstable—within a very short period the original components are separated.

Hydrophilic systems on the other hand exhibit some affinity for water. The hydrophilic colloids absorb water and swell up. Most of the colloidal systems occurring in plants are of this type. When both the phases in a colloidal system are liquid it is called an *emulsion*. An

emulsion generally belongs to the class of hydrophilic system. When two immiscible liquids are vigorously shaken, an emulsion can be prepared. Emulsions are of two types—oil-in-water and water-in-oil. Of these, the former is more common than the latter. Milk, cream, latex etc. are the best examples of oil in-water type.

A colloidal system when exhibits the property of fluid consistency is known as *sol*, which can be poured easily from one container to another. If the system is more rigid and viscous having a semi-solid consistency it is known as *gel*. Whether a colloid takes the form of a sol or a gel depends on the concentration and the temperature. Thus the suspension like clay-in-water or emulsion like milk, latex etc. are the examples of sol ; whereas the table jellies, pudding etc. are the examples of gels.

Since the increase in viscosity results in a change of physical state of substances, a sol can easily be converted to a gel. Thus the white of an egg is a sol under normal condition which, however, forms a gel on heating. The gelatin-water is a sol when it is prepared by heating, on cooling, however, it forms a gel. When this gel is heated with water, it again forms a sol. This change of state from sol to gel is known as *gelation* and that of a gel to sol is known a *solution*.

2.4 Properties of colloids : (i) *Heterogeneity*—The colloidal solutions are physically heterogeneous whose properties are intermediate between a true solution and a coarse dispersion. This is because the colloidal substances are intimately mixed but not molecularly dispersed with one another.

(ii) *Incapable of passing through parchment membrane*—In a colloidal solution since the particles are less than $100m\mu$ but greater than $1m\mu$ in diameter they pass through the pores of the filter paper but not through the membrane of parchment paper or collodion ; whereas the solute particles of a true solution pass through these pores. According to Graham, even when diffusion takes place, the rate of diffusion is very slow in case of colloidal particles.

(iii) *Adsorption*—Concentration or retention of some molecules or ions at the surface of another is generally known as adsorption. Some consider adsorption as a purely physical process ; others, however, consider that chemical forces play an important role in attracting and holding the absorbed molecules. The absorbed substances can be removed by the application of certain amount of energy. Adsorption is an universal occurrence at the interfaces of colloidal systems.

(iv) *Tyndall phenomenon*—This term has been coined after its original discoverer, John Tyndall. This phenomenon results owing to scattering or diffraction of light. When a beam of strong light passes laterally from one side of a flat parallel faced glass vessel filled with colloidal solution, the path of light can be distinctly seen as a cloudy opalescent track through the solution. If, however, the light is passed through a true solution, its path cannot be observed. This

effect, therefore, is one way of distinguishing a colloidal suspension from a true solution. This effect of scattering light demonstrates the heterogenous nature of the colloidal substances.

(v) *Brownian movements*—It has been found that any particle whose diameter falls between $4\text{-}5\mu$ exhibits a peculiar movement when suspended in water. This phenomenon of highly erratic movement of suspended particles is known as Brownian movement after the name of the discoverer.

This movement was first noticed by Robert Brown (1828) while studying the pollen grains under microscope. This is due to irregular bombardment of particles by the molecules of the liquid in which these are suspended.

(vi) *Coagulation or flocculation or precipitation*—Since the colloidal particles are in a state of continuous movement (Brownian movement), repeated collisions result among the particles, as a result the particles agglomerate, giving rise to larger masses that eventually settle out of the surrounding medium. This phenomenon is called coagulation or precipitation.

Precipitation is irreversible in nature and a drastic treatment is required to bring about redispersion.

Colloids can be protected from precipitation by the presence of another colloid. One colloid forms a protective layer around the particles of other colloids.

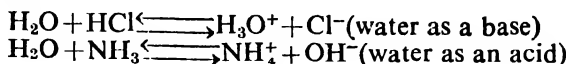
(vii) *Viscosity*—Viscosity is the internal friction or resistance in a fluid tending to prevent its flow. The rate of flow of liquids is less if the viscosity is high. The viscosity is influenced by temperature—normally it varies inversely with temperature.

(viii) *Electrical properties*—The dispersed particles of a colloidal system carry electrical charges and all the colloidal particles in one colloidal system carry charge of same nature and consequently repel each other. This keeps the colloidal particles dispersed.

A colloidal system is electrically neutral, for every charge carried by the particles an equal charge of opposite value is carried by the ions of dispersion medium. So basically it is similar to a solution of an electrolyte, but still they (colloidal systems) behave differently in that the particles migrate as a whole to one pole or the other depending on the charge and never separate as positive or negative ions as in electrolytic dissociation. This phenomenon of migration of particles is known as *cataphoresis* or *electrophoresis*.

(ix) *Amphiprotic properties*—Some solutions (gelatin, sol etc.) like protein solutions are amphiprotic in nature *i.e.*, which act either as an acid or as a base *i.e.*, it can donate or accept a proton. Amino acids, components of protein molecule are good example of amphiprotic, as they can act both as weak acids or weak bases. Water can also

act as a base in the presence of HCl and as an acid in the presence of ammonia :



2.5 Protoplasm is a colloidal system : Many theories have been proposed to explain the structure of the living materials within the cell. One of them is the reticular theory which considers the material as fibrillar. Granular theory considers it as granules and alveolar theory which accounted for the emulsion-like appearance of some cells. In 1925 Wilson, however, proposed the *colloidal theory of organization* of the cell substances. Experimental evidences of Anderson (1957), Gross (1957) and others clearly support the colloidal theory of cell structure.

Protoplasm is the living substance of the cell, which is a colourless fluid in which numerous small granules and droplets of insoluble materials are present. The most peculiar fact of the protoplasm is that it forms a most complex colloidal system (Heilbrunn, 1958). In plant cell, since all the particles in the disperse phase are not alike, the cytoplasm is said to be a *polyphasic* colloid.

That the protoplasm is a colloidal system can be proved clearly from the properties of protoplasm. Like colloidal solution or sol the particles or granules present in the cytoplasm are in a dispersed or discontinuous stage consisting of either very large molecules or of aggregate of small molecules. The diameter of these particles according to Heilbrunn ranges between 3 and 4 μ .

Protoplasm exhibits the properties of both suspension and emulsion. The dispersed or discontinuous phase is of protein molecules if it is a case of suspension or of fatty acid molecules if it is a case of emulsion and the continuous phase is simply water or water mixed with other mineral substances.

Generally, protoplasm shows the character of liquid i.e. solution but in some cases it becomes more rigid and viscous and appears as a somewhat stiff gel. The condition of changing sol to gel consistency within the protoplasm takes place frequently, particularly during the formation of plasma membrane and in nuclear sap (in the formation of nuclear fibre during cell division). Heilbrunn (1958) suggested that this rigidity is due to coagulation process catalysed by a specific enzyme. Different degrees of coagulation accounting for different degrees of structural rigidity.

The property of viscosity of protoplasm, like colloids is another proof that protoplasm is a colloidal complex. The cytoplasmic viscosity varies greatly under different physiological and environmental conditions, presumably in the living state some structure always remains, even in a state of low viscosity. The paradox of cytoplasm behaving like a liquid while displaying the structural properties suggestive of a solid scaffolding can be explained on the basis of its being a colloid.

Heilbrunn showed that the granules of the protoplasm exhibit a peculiar constant movement due to the irregular bombardment of the particles. These movements of particles are much similar to the Brownian movements exhibited by the colloidal particles.

The colloidal system of protoplasm again can be proved by the fact that the particles of the dispersed phase carry an electric charge *i.e.* it exhibits the electrical properties of colloidal system. It has been observed by Hardy that when electric current is passed in onion root tip, protoplasm passes to the side nearer to the negative pole. Those particles that move towards the negative pole carry the positive charge and this phenomenon is known as cataphoresis. Since the cell is a polyphasic colloidal system it is not difficult to comprehend the occurrence of many separate chemical reactions within the cell at physiological temperatures. The selectively permeable membranes surrounding certain discrete structures like endoplasmic reticulum, mitochondria, Golgi complex are playing an important role in separating the major reactive system of the cell. Since the cell is in a polyphasic colloid, one phase may attract one set of reactions while the another phase may attract other reactions. So, wide diversified biochemical reactions of entirely different characters occur simultaneously in each of the cell organelles.

When the protoplasm fails to exhibit all the properties of colloidal system we call then, the cell to be "dead." Under these conditions the protoplasm loses its viscous consistency and coagulates to form a solid mass. It is no longer the protoplasm of our conception and under the condition all the cell activities come to an end.

SELECTED QUESTIONS

1. What are colloids? How can they be distinguished from crystalloids? Describe the properties of colloids.

Refer articles 2.1, 2.2 and 2.4

2. What are colloids? Give a brief account of the nature and properties of colloids.

Refer articles 2.1, 2.2 and 2.4

3. What are the three most outstanding characteristics of colloidal systems in which water is the dispersion medium?

Refer article 2.4

4. "Protoplasm is a colloidal complex"—Discuss.

Refer article 2.5

5. Describe some of the phenomena characteristic of colloidal systems which occur in plant cells, citing specific examples.

Refer articles 2.4 and 2.5

6. Write notes on Brownian movements.

Refer article 2.4 (v)

CHAPTER 3

Cell Structure and Function

3.1 Short history of living cell : *A cell¹ may be defined as the basic structural unit of a living organism and is the common denominator of a living body.*

The word "cell" was first coined by the English physicist and mathematician Robert Hooke in 1665 to designate the tiny structures present in a piece of cork (the bark of Mediterranean oak). Hooke himself found that in many living bodies the cell was filled with a liquid material. In later years, a Czech physiologist Johannes Purkinje (1787-1869) gave the name to this complex fluid—*protoplasm*. This was however later supported by Hugo von Mohl (1846). In 1833 Robert Brown found the presence of small bodies within the epidermal cells of certain plants which he called *nuclei* (singular *nucleus*). However the enunciation of the "cell theory"—the basic aspects of which hold good even today—goes to the credit of two German scientists Matthias J. Schleiden (1838), a botanist and Theodore Schwann (1839), a zoologist.

Some twenty years later (1860) Rudolf Virchow made another important observation that cells come only from pre-existing cells.

With the gradual advancement of science and availability of improved tools and techniques of analysis the concept of a cell has been vastly elaborated. In 1920 the main parts of a cell which consists of a cell wall, nucleus, vacuoles and cytoplasm have been discovered. With the discovery of electron microscope and phase contrast microscope the concepts of a cell has been completely changed and has opened up a new domain to the cytologists and cell biologists.

3.2 Sub-cellular particles : *The minute structures in plant or animal cells which are beyond the power of a normal light microscope and can only be studied through electron microscopy are termed as sub-cellular particles.*

It is impossible to imagine any biological activity that does not involve a chemical reaction. The cell, therefore, can be considered as a chemical factory capable of performing all the services and of manufacturing all the products necessary to continue life. Although for every specific function within the cell there are specific structures some of which appear as small granules under a standard light microscope. But gradually with the advent of electron microscopy early in the 1950 biologists have been able to accumulate a good deal of information about the fine structures of the cell and its function at the molecular level (Fig 3.1).

The term "cell inclusions" covers a wide range of structures in the cell—apart from the nucleus and the vacuole. These can be divided into two groups: one those which contribute to the metabolic activity of the cell and can be called the *protoplasmic organelles* of the

¹ "The cell can be defined as the smallest organised unit of any living form which is capable of prolonged independent existence and replacement of its own substance in a suitable environment.—John Paul (1965) in *Cell Biology*.

cell ; the other group include the inert, non-protoplasmic products of metabolism which are known as *ergastic substances*.

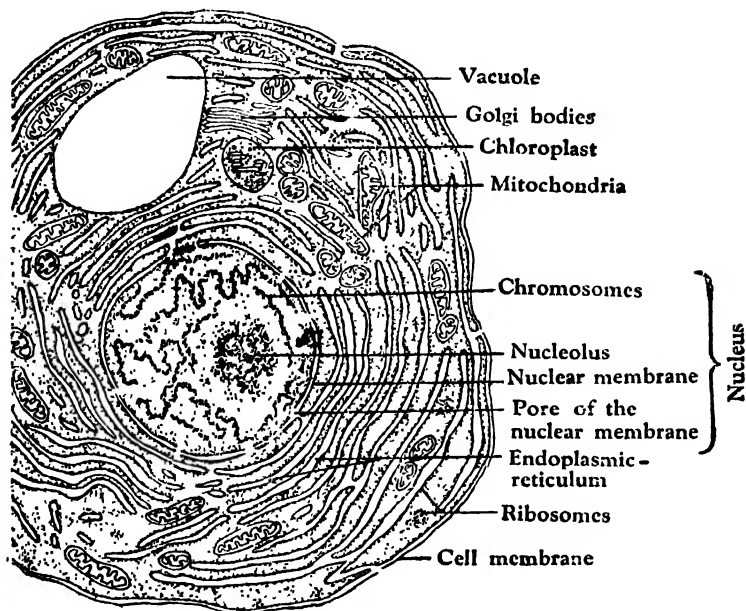


Fig 3.1 An enlarged generalized cell, as seen with an electron microscope showing the various structures within it.

The protoplasmic organelles are mainly the *plastids*, the *mitochondria*, the *endoplasmic reticulum*, the *ribosomes* and the *Golgi complex*. The ergastic substances include organic storage products e.g. *starch grains*, *aleurone grains*, *oil droplets*, *tannins* etc. and inorganic substances like *calcium oxalate crystals* and *silica deposits*.

It is the protoplasmic organelles which are the main site of all the biochemical activities that are continuously taking place within the

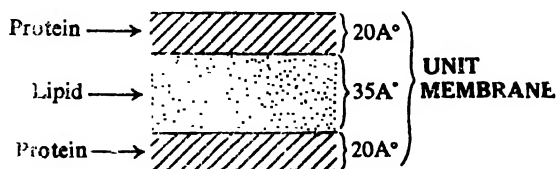


Fig. 3.2 Lipoprotein three layered structure of the unit membrane.

cell to continue life. The outermost region of the protoplasm is the *plasma membrane*. The cell membrane is generally assumed to be

a double layer of protein substances with lipoidal substances sandwiched between these two protein layers (Fig. 3.2). This membrane is 70-100 Å¹ in diameter. The lipid layer is said to be impermeable. For the selective permeability there is a number of pores which allow certain smaller substances to enter but not the larger molecules. The lipoidal material in the centre of the membrane is probably the principal barrier to the passage of solutes into the cell. The membrane which allows certain substances to enter while restraining others is known as *differentially permeable*.

The cell membrane consists of single unit membrane while the double membraned envelope of the mitochondrion and chloroplasts consists of two unit membrane in paired arrangement and in close apposition. Other sub-cellular particles like endoplasmic reticulum,

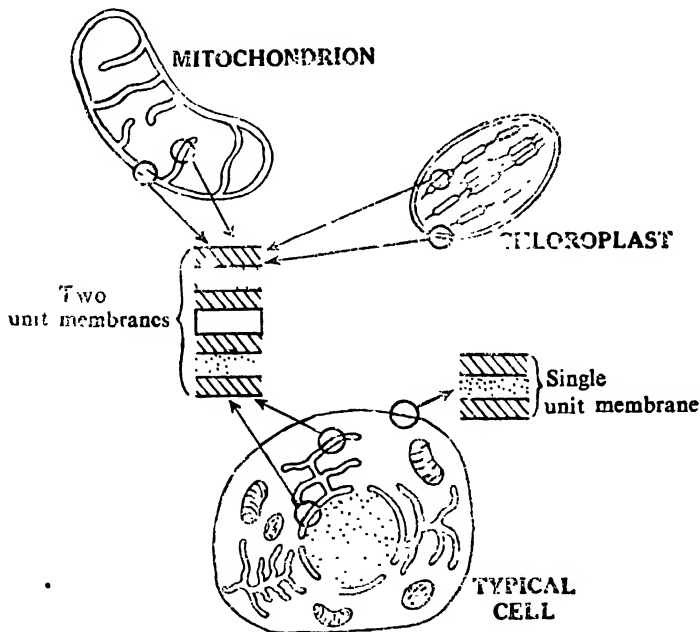


Fig. 3.3 Diagrammatic representation of the various arrangements of unit membrane in the organelles of a typical cell.

Golgi complex and nuclear envelope are also two unit membrane structure. The individual grana of the chloroplasts are multilayered structure made up of unit membranes closely packed and stacked on top of one another (Fig. 3.3).

A. PLASTIDS : CHLOROPLASTS—Plastids are microscopic organelles found in plant cells. There are different types of plastids. Leucoplasts

¹ A (Angstrom) = $\frac{1}{10,000}$ part of a micron (μ) or 0.1 m μ or 10^{-8} cm

are the colourless plastids contain starch grains. Chloroplasts contain the green chlorophyll and chromoplasts contain other pigments. Of all these plastids chloroplasts are most important in plant cells. These are characterised by their greenish colour due to the presence of chlorophyll *a* and *b* along with carotenoids and xanthophylls. They are found in all photosynthesizing organisms except blue-green algae and photosynthetic bacteria. The chloroplast is, therefore, the centre of photosynthetic activity. They are found in the spaces of the ground cytoplasm and their number may vary from one, as in some algal cells, to a very large number in cells of higher plants.

The chloroplasts are bound on the outside by a double layered semipermeable membrane (peristromium) about 150A thick. The chloroplasts are enormously variable in shape, but in higher plants

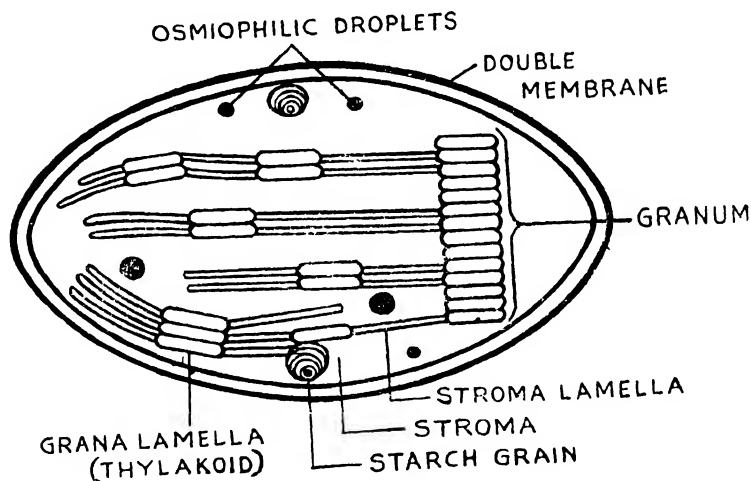


Fig. 3.4 Internal structure of a chloroplast.

they show a certain conservatism of structure. They are circular or ovoid in top view (about 6μ in diameter) and discoidal or ellipsoidal, more or less like a plano-convex lens in side view (about $2-3\mu$ thick). Under high power microscope (Fig. 3.4) the chloroplasts reveal the presence of disc shaped green proteinaceous matrix known as **grana**¹ dispersed in a colourless stroma or matrix. It also contains starch grains and osmiophilic droplets. Double membraned lamellae stacked upon one another cover the width of the chloroplast and can be differentiated into *stroma lamellae* and *grana lamellae*. In cross section these lamellae form sac-like structure, called *thylakoids*. The lamellae membranes or thylakoids are composed of protein and

¹ Grana—this morphological subunit has been termed as *quantosome* by Park *et al* (1963).

lipids and the chlorophyll is associated in between protein and lipid portions (Fig. 3.5). The stroma lamella is much thinner than the

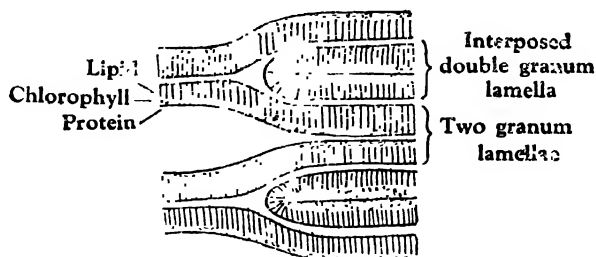


Fig. 3.5 Organisation of the chloroplast lamellae.

grana lamella and is composed of unpigmented lipoproteins and associated enzymes involved in the secondary reactions of photosynthesis (Granick, 1963).

The grana are roughly circular in top view and made up of stacks of disc shaped lamellae like piles of coins; they are about 400-800 $m\mu$ in diameter and 400-900 $m\mu$ in height. The number of discs per granum is often between 20 and 30 but sometimes upto 100. The size and number of grana in a chloroplast varies in different species, but generally there are 20-100 grana in each chloroplast. The chlorophyll is more concentrated in the grana than in the stroma.

According to Street (1963), chemical composition of dry chloroplasts reveals 40-50% protein, 23-25% phospholipid, chlorophyll *a* and *b* 5-10%, carotenoids 1-2% and about 5% RNA. Several enzymes are also present in the chloroplasts and their amount in the plastids depends on the level of maturity of the plastids. As a cell attains maturity, other enzymes including those concerned in the synthesis of chlorophylls, carotenoids etc. begin to accumulate gradually.

Functions—As already stated the chloroplast is the site of photosynthesis. The specialised lamellar structures provide a proliferation of membrane surface. The complicated events during photosynthesis require such specialised "spatial arrangement of chlorophyll, associated pigments and of enzyme systems, so that light energy is efficiently trapped and stored, in compounds from which other forms of energy may later be derived for the benefit of the organism concerned."

The production of carbo-

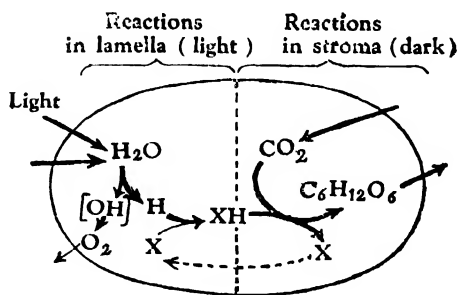


Fig. 3.6 Essential reactions in a chloroplast. X represents carrier molecule.

hydrates from water and carbon dioxide in the presence of light and chlorophyll in the chloroplasts (i.e. photosynthesis) consists of two main series of reactions. The first is *photolysis (light reaction)* i.e. splitting of water in the presence of light and chlorophyll to give H and OH fractions, the former reduces a carrier substance (X) and the OH fraction is released as oxygen gas. The second is a *dark reaction* involving CO_2 fixation. Here the reduced carrier (XH) ultimately reduces CO_2 to a monosaccharide through a large series of reactions and itself becomes oxidised again (X) and a good deal of energy (ATP) is produced (Fig 3.6). At least two series of enzymes are involved, one concerned with the 'light reaction' is bound in the grana and that of 'dark reaction' free in the stroma proper (For detail refer Chapter 9).

B. MITOCHONDRIA—The history of mitochondria dates back as early as in 1898 when Benda first discovered the occurrence of mitochondria in the living cells. It is present both in higher plants and animal cells, but not in bacteria. Benda had shown mitochondrial staining action with alizarin and crystal violet, but in 1900 Michaelis demonstrated their selective staining by Janus green.

The term mitochondria was not accepted immediately after its discovery. Like Golgi complex they have been termed variously as chondriosomes, plasmosomes, plastosomes, fuchsinophilic granules, parabasal bodies etc. For many years the term chondriosomes has persisted but this too completely wiped out in the present day-usage.

The number and size of mitochondria vary in cells. They may have 200-300 mitochondria, but they may vary considerably from a few to 1000 or more. Some algal cells may have only one mitochondrion. Mitochondria have an unique appearances. In some cases they are filamentous, diameter size may be $0.2-1\mu$ and length may vary from 2 to 10μ . They may be ring-shaped, round or spherical in appearance,

In 1952 Palade observed that mitochondrion has an outer membrane and an inner membrane under electron microscope. These two membranes are separated by a space containing a fluid matrix by about 75A thick. The inner membrane forms many infolding which have been termed as *cristae* (sing. *crista*) by Palade. In plants these cristae frequently form closed loops by connecting with one another. The space between outer and inner membrane is about 80—100A wide. The cristae usually run at right angle to the long axis of the mitochondrion. The space in which these infolding lie is filled with dense fluid material with no definite structure in it.

Like all unit membrane, each of the two membranes of the mitochondrion has an inner lipid layer and bounded by two outer protein layers. The outside of the outer boundary is made up with small stalkless sphere packed closely together to give a rough or pimpled appearance of mitochondrial surface. The particles of the

inner membrane have a base, a stalk with a spherical head (stalked particles). The stalk is about 50\AA long and 30\AA wide and the head is about 80\AA in diameter. The entire length of the structure is about 160\AA . The distance from the centre of one head piece to

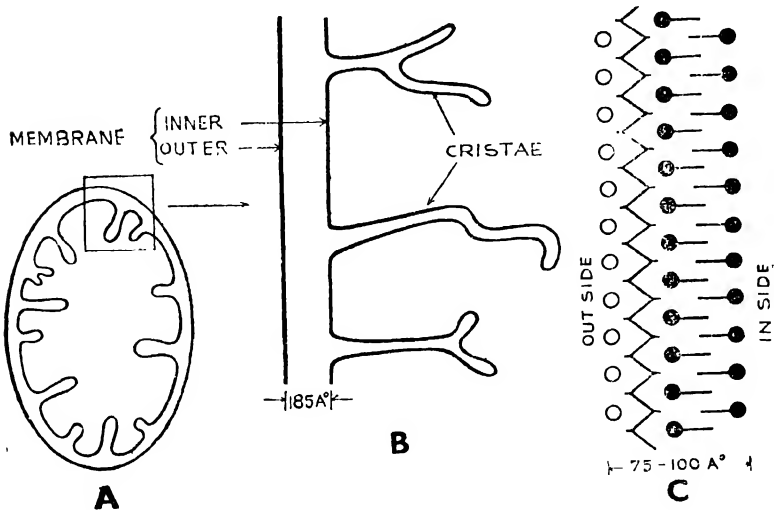


Fig. 3.7 A—Structure of a typical mitochondrion.

B—Double membrane structure of a mitochondrion with infoldings forming cristae.

C—Lipoprotein nature of the membrane. Hollow spheres are protein layers lined by a double layer of lipid molecules (black stalked spheres).

the centre of its neighbour is about 100\AA . That means a 20\AA space between these particles suggesting a major role of mitochondria. These are, therefore, the 'electron transport particles'. Very recently some small particles have been found to be present on the wall of the cristae—**oxysomes**.¹ These particles are mainly concerned with the electron transport system in respiration.

Functions—Mitochondria have been shown to possess the ability to catalyze the reactions of the Krebs' cycle using pyruvic acid as fuel. As a result of the cycle, pyruvic acid is completely oxidised to carbon dioxide and water with the release of energy. The oxidation involves the release of electrons from the substrate by appropriate electron acceptor like NAD^+ or NADP^+ . These electrons are then passed to molecular oxygen via cytochrome. The energy released by this electron transfer system is conserved, in part at least by coupling oxidation with the phosphorylation of ADP to form ATP. This

¹ The term "oxysomes" has been used to describe the basic macromolecule assembly of enzymes controlling the complete transport of electrons from substrate to molecular oxygen and the generation of ATP (Chance *et al*, 1963).

process is known as *oxidative phosphorylation* and the energy thus produced can be utilized by the cell through the cleavage of the terminal phosphate of ATP to give ADP and energy. They are also said to play a role in the oxidation of long chain fatty acids to carbon dioxide and water. Thus 90 percent of ATP is formed in mitochondria (Lehninger, 1959). So, mitochondria is said to be the "power-house of the cell" (Siekevitz, 1957).

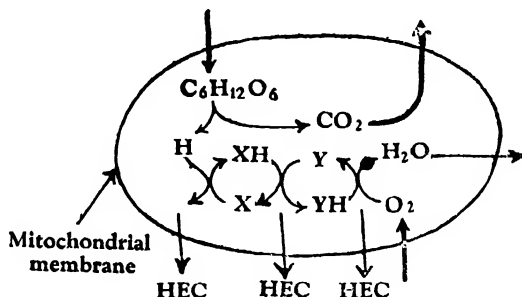


Fig. 3.8 Essential reactions in a mitochondrion. X and Y represent carrier molecules. HEC signifies high energy compound.

Most of the enzymes concerned with the substrate reactions of Krebs' cycle are easily extracted in soluble form following disruption of the mitochondrion and hence are considered to be located in the inner matrix of this organelle (Lehninger, 1959) (For detail refer Chapter 15).

C. ENDOPLASMIC RETICULUM—Apart from mitochondrion there are certain much branched systems of canal like double membrane structure on which ribosomes are found to be present as localised swellings and are known as *endoplasmic reticulum*. It is present only in higher plants and absent in bacteria, fungi and lower groups of plants.

The three principal forms of endoplasmic reticulum are *cisternae* (lamellae), *vesicles* and *tubules*. The cisternae are the long flattened units 35-50 $m\mu$ in thickness. The vesicles are rounded in shape having the diameter 27-500 $m\mu$ and the tubules are very much irregular in their appearance having the diameter 50-100 $m\mu$. In all these types of reticulum the spaces enclosed by the membrane comprise a vacuolar system and form a channel for the movement of the materials. The membrane of endoplasmic reticulum is very much comparable to that a plasma membrane. It consists of lipoprotein with the property of permeability and transport like that of plasma membrane. The endoplasmic reticulum is sometime continuous from nuclear membrane to the plasma membrane.

Functions—The functions of the endoplasmic reticulum vary with the form and location. The important function is that they increase surface area within the cytoplasm for various metabolic activities and its peculiar vacuolar system helps the easy transport of the metabolites

and accumulates them in the vacuoles for storage. They also possess osmotic properties restricting entry and exit of materials. The canalicular system allows intercommunication between the outside and inside of the cell. Endoplasmic reticulum is also linked with the transmission of impulses or excitations within the cell like muscle and nerve cells. It also helps for the orderly distribution of enzymes. Reticulum contains enzymes responsible for the synthesis of certain lipids and therefore play an important role in lipid metabolism (Siekevitz 1963, '65). They also contain enzymes involved in glycogen synthesis (Freeman, 1966).

The membranes of endoplasmic reticulum also possess an electron transport system (Siekevitz, 1965).

D. RIBOSOMES—In 1953 Palade first observed the presence of some particulate units in the ground substance. They appear as electron-opaque bodies about 150A in diameter.

Ribosomes are universally present in all plant and animal cells as no alternate mechanism for protein synthesis has been established. In most prokaryotic cells¹ ribosomes have been found with a sedimentation coefficient ($S \equiv$ Svedberg unit) of the 70S type whereas the ribosomes of eukaryotes (nucleated organisms) were about 80S (Taylor and Storck 1964). It is usually composed of two subunits—one 50S and the other a 30S. Both the 50S and 30S subunits contain 63-64% RNA and 36-37% protein. Ribosomes are, therefore, often been called as ribonucleo protein (RNP) particles.

In relation to size and composition the ribosomes of plants tend to resemble those of animal cells, rather than those of bacteria. Ribosomes occur freely either in the general mass of the ground substance or bound loosely on the outer membrane of the endoplasmic reticulum. Their number in a cell varies considerably whether they are in a free or attached state. It is especially large in an active cell and considerably small in less active cell.

The average diameter of the particles ranges from 100-150A. They may float freely in the cytoplasm or may be bound to the outer membranes of the endoplasmic reticulum and its vesicles.

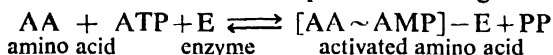
Functions—Ribosomes or microsomes² are the principal sites of protein synthesis (first proposed by Brachet, 1941) and fatty acid metabolism in the cell. They are usually formed in the nucleus and move to the cytoplasm thus providing a continuity between the genetic information from the nucleus and the actual production of individual enzymes in the cytoplasm.

¹ The prokaryotes are generally lacking a membrane around their nucleus and have no well defined membrane-limited organelles. The eukaryotes on the other hand have a membrane around their nucleus and hereditary material is found in chromosomes. They have well defined membrane-limited organelles.

² Under high speed centrifugation a fraction containing the endoplasmic reticulum and its ribosomal content can be separated. This fraction represents the functional unit and is termed as *microsomes*.

Brachet (1941) was the first to suggest the role of ribosome in protein synthesis.

The first step is considered to be the enzyme catalyzed activation of amino acids. This reaction takes place according to :



The second step is considered to be the addition of specific nucleotides to end grouping of RNA in the soluble portion of the cytoplasm. The third step involves the binding of the activated amino acid to the RNA of the soluble fraction which now possesses specific nucleotide end grouping. The final step is believed to involve the transfer of this complex to the ribosome, followed by polymerization of the amino acids to produce protein (Stephenson *et al*, 1959) [For detail refer Chapter 10].

E. GOLGI COMPLEX—Although their presence as cell organelle was known for a long time in animal cells, these have been seen in plant cells only in recent years with the help of electron microscope. It is now found to be present in all eukaryotic cells.

The Golgi complex has been a controversial issue in cell structure since 1898 when it was first discovered by Camilo Golgi. According to some the Golgi complexes was an artifact resulting from prolonged fixation of cells. But it has been now established that Golgi complexes are definite organelle of the cells. They have been given different names as dictyosome, golgiosome, apparatus, body, complex etc. Of all these names, the one most used at the present time are apparatus and complex.

The Golgi complex is a disc-shaped organelle composed of unit membrane. Like endoplasmic reticulum it is a canalicular system with sacs. The surface of the canal and sac is smooth. The Golgi complex consists of a number of membrane bounded spaces arranged in strictly parallel rows, stacked one upon the other like a pile of saucers and associated with a group of more of spherical vesicles at their margins. The number may vary from one to many in each cell.

Functions—The functions of the Golgi complex are obscure, possibly they are concerned with some complex enzymes synthesis and also with the regeneration of membrane systems in the cell. Their number seems to increase during cell division, while the early stages of differentiation are marked by their disappearance.

CELL PHYSIOLOGY

3 3 Entry and exit : All living cells are bounded by cell membrane—the outermost living boundary of the cell, outside which lies the environment. Since the body of the higher plant consists of specialised cells—each of which empowered with specific functions, for all of which they require a number of elements from the environ-

ment. Through this membrane, therefore, must pass all the elements and other substances which the cells obtain from the environment, as well as it must allow everything that the cell returns to the environment. So one of the most vital problems of cell physiology is the problem of entry and exit of those materials. So long as the cell is alive, this type of entry and exit takes place continuously through the cell membrane.

Since the plant cell contains a rigid wall in addition to its membrane, the solid particles can not pass in or come out from the cell. The substances that pass must be in a liquid or gaseous form. The way in which the gases or liquids enter the cell from the environment or move from one cell to another is not definitely known, but that some physical processes must play a role in their movements is clear. So understanding of these physical processes will be helpful in understanding the nature of entry and exit of gases and liquids from the environment.

(i) **IMBIBITION** :—Many seeds whose seed coats are not impermeable to water, if immersed into water, will soak up water and swell up considerably. *This phenomenon of swelling up of seeds when brought in contact with water is known as imbibition.* Many other substances like gum, agar, cellulose, gelatin etc. exhibit this property of uptakes of water molecules from the surrounding medium. Such materials swell not only by taking water in liquid form but also by taking water in vapour form. Thus the swelling of wood-work during rainy season is also a familiar example of imbibition. Since the cell wall and the protoplasm possess this property, imbibition plays an important role in the metabolism of the cell.

Imbibition of the materials causes an increase in volume of the imbibant, although the total volume of the imbibant and water molecule is always less than the initial volume of the imbibing substances and water molecules. This decrease in the final volume is due to compression during imbibition.

Considerable amount of energy in the form of heat is liberated due to imbibition. If some starch is allowed to imbibe water in a calorimeter, a change in the temperature reading will be recorded.

A considerable amount of pressure will be developed by the swelling imbibant kept in a confined vessel. This is known as *imbibitional pressure*, which means the actual pressure developed as a result of imbibition.

Basically, imbibition may be considered due to diffusion and capillary phenomenon, but fundamentally it is due to the differences in diffusion pressure between the liquid in the external medium and the liquid in the imbibant. Water or the liquid will move constantly to the imbibing material as long as the diffusion pressure in the water or liquid medium is less than the liquid in the imbibant and an equilibrium will be reached when the values of the diffusion pressure attain the same level in both the cases.

(ii) **DIFFUSION** :—"The molecular theory of matter" states that all matters are formed with some small particles known as molecules which are in a continuous motion. In case of gas or liquid, movements of the molecules are at random, still they have a tendency to move from a region of higher concentration to the region of lower concentration until the molecules are evenly distributed throughout the available

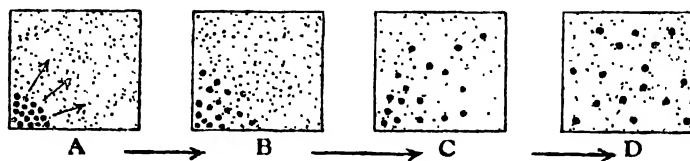


Fig. 3.9 A-D Stages of diffusion indicating the spreading of molecules as indicated by arrows in the medium.

space. This spread of molecules from its more abundant place to a region of less abundant place is known as **diffusion** or in other words it may be defined as a movement of molecules from regions of high partial pressure to regions of low partial pressure as a result of their inherent kinetic energy as shown in Fig. 3.9 A-D. This phenomenon is exhibited by the molecules of gases, liquids, as well as by those of solids. Diffusion of ions also occurs and even colloidal particles diffuse but very slowly.

Importance of diffusion in plants—The velocity of diffusion is dependent on a number of factors like temperature, viscosity, as well as the relative size of the particles.

The diffusion of the gases sometimes results in the development of a pressure which may be defined as **diffusion pressure**. The magnitude of the pressure is proportional to the concentration of the diffusible particles i.e. the greater is the concentration of the particles the greater is their diffusion pressure. The molecules of liquids and solutes are less abundant than the gases and since the liquids and solutes exert diffusion pressure, it is convenient to express the phenomenon of diffusion as the movement of the molecules of a substance from a region of higher to a region of lower diffusion pressure.

In biology, the process that concerns us most is the diffusion of substances dissolved in water. All living cells exist in an aqueous environment and are separated by cell membrane with a mixture of things of the environment by watery content within the cell. The cell membrane is said to be *differentially permeable* as it allows only certain substances to pass but not all. For substances to which the membrane is permeable, entry and exit is a matter of diffusion. The cell membrane although slows down the rate of diffusion process, but it does not affect the direction of movements.

The diffusion process is of immense importance in biology. We cannot imagine any physiological process which directly or

indirectly does not involve the phenomenon of diffusion. All the aerial intake of different gases i.e. carbondioxide and oxygen from the atmosphere as well as the movements of gases in the intercellular spaces of the cells take place by this process. Intake of water and mineral substances from the soil by the higher plants also takes place practically by the process of diffusion although a more complicated mechanism is involved in their entrance by the roots.

Loss of the molecules from the plant body is also related with the process of diffusion. Thus the loss of water molecules in transpiration and also the loss of gases like carbondioxide and oxygen according to circumstances takes place by diffusion. The vapours of volatile liquids also diffuse in the same way.

(iii) **OSMOSIS** :—It may be defined as *the movement of molecules of a solvent from a region of high partial pressure to a region of low partial pressure when the two regions are separated by a semipermeable membrane i.e. a membrane permeable to solvent molecules but not to solute molecules.*

If, however, two solutions of different concentration are separated by a sheet of rubber, no movement of solution will take place in either direction. Such a membrane through which nothing can pass is known as *impermeable*. If instead of rubber sheet, a piece of filter paper is placed between the two solutions, all the molecules will move freely through it, ultimately the level of the liquid will remain unchanged. Such a membrane is known as *permeable*. If, however, parchment paper is placed between the solutions, water molecules or other molecules of the solutes from lower concentration will move to the higher concentration. As a result of this movement the level of the solution having higher concentration will rise and the level of the water or low concentration side will fall. Such a membrane which allows only water to pass and not the other substances is known as *semipermeable* membrane. Therefore, the diffusion of water through such a membrane is the main basis of osmosis.

True semipermeable membrane is a very rare occurrence, as very small amount of solutes also passes out through this membrane, although the rate of diffusion of the solutes is much less than the rate of movement of solvent. Such a membrane is, therefore, better called as *differentially permeable*, which will allow some solutes to pass but will hold back others.

In living systems most of the cells act as an osmotic chamber where the non-living cell wall and the living plasma membrane act as a differentially permeable membrane through which water molecules pass easily whereas the particles can not pass. Besides cell membrane other naturally occurring semipermeable membranes are fish bladder and the white membrane of eggs (after removing the hard calcium carbonate coat with mineral acids).

As osmosis occurs between two solutions of different concentration the process will continue till the concentration of these solutions

is equalised. As a result of this, the hydrostatic pressure will be sufficient to stop any flow of liquids. This is known as **osmotic pressure**. This pressure, is therefore, equal to the pressure which must be applied to the solution just to prevent the osmosis. Osmotic pressure may be defined as an index of certain properties of the solution rather than the actual pressure exerted by the solution. If the osmotic pressure of a sugar solution be defined as 5 atmosphere at a particular temperature, obviously that does not mean that the solution is actually exerting a pressure of 5 atmosphere but it means that it has got certain osmotic properties which will be apparent under particular circumstances. This pressure is more potential rather than the existing capacities.

Osmotic pressure of a solution may also be defined as the excess hydrostatic pressure which must be applied to it in order to make its water potential equal to that of pure water. Since no actual pressure is developed unless the solution is placed in an osmometer it is preferable to use the term *osmotic potential* instead of osmotic pressure. Osmotic potential (symbolised as $\pi=pi$) is given a negative sign and it is then equal to the water potential of a solution at atmospheric pressure. Osmotic potential can be accurately determined by

$$\pi = -12.04 \Delta T$$

Where ΔT is the freezing point depression of the solution.

Methods of measuring the osmotic concentration of cell: There are three methods for determination of osmotic pressure viz., (a) plasmolytic method (b) cryoscopic method and (c) vapour pressure method.

(a) *Plasmolytic method*—The basic principle of this method is to determine the exact concentration of the cell (C) from the external solution which just brings about (incipient) or fails to bring about the plasmolysis in the cell.

It is done by placing thin sections of tissues into graded sugar solutions (0.02 to 0.05 M). If the solution are so graded that both severe plasmolysis and lack of plasmolysis are observed, then there must be a solution where approximately half of the immersed cells will exhibit plasmolysis. This value is, therefore, considered as OP at incipient plasmolysis condition.

The osmotic pressure (OP) of a solution can be calculated by the following formula.

$$OP = CRT$$

Where C is the molar concentration, R is the gas constant (0.082) and T is the absolute temperature (273 + °C). So, the OP for one molar sugar solution at 0°C will be

$$\begin{aligned} OP &= 1 \times 0.082 \times 273 \\ &= 22.4 \text{ atmosphere} \end{aligned}$$

So, one molar solution of sugar when separated by means of a semipermeable membrane has an OP 22.4 atmosphere at 0°C.

(b) *Cryoscopic method*—There is a direct proportionality between the osmotic pressure, boiling point elevation, vapour pressure lowering and freezing point depression of solutions. The OP of the plant cell can also be determined by

cryoscopic method which consists of determining the freezing point depression of the cell sap and then calculating the OP by the formula.

$$OP = \frac{22.4}{1.86} \Delta \text{ or } OP = 12.04 \times \Delta$$

Where Δ stands for freezing point depression.

This can be determined by placing the extracted sap in a test tube which is placed in a freezing bath. A freezing point thermometer is immersed in the test tube with a stirrer around the bulb. The sap is agitated as the temperature slowly decreases. The sap is undercooled to a critical temperature. Suddenly there is a release of heat of crystallization which causes the temperature to rise rapidly and then to level off at the true freezing point. According to Harris and Gortner (1914) a correction is applied because of the undercooling.

(c) *Vapour pressure method*—This is based on “properties of the solution colligative with osmotic pressure.”

In practice, a droplet of the sap or solution of unknown osmotic concentration is put in a glass capillary tube, followed by an air column and a droplet of sucrose solution of known concentration. Several tubes with varying concentration of sugar solution are prepared and they are sealed properly. The length of the sap column is measured both before or after equilibrium is reached.

The results are plotted in a graph and the concentration which produces no change in the length of the sap column is the isotonic solution of known OP.

It may be noted that often there is a discrepancy between the osmotic pressure determined by the plasmolytic method and that determined by cryoscopic method, the former being higher than the latter. The larger value determined by plasmolytic method is considered to be due to the presence of a “non-osmotic water absorbing component.”

It has also been observed that vacuolar volume of a cell when immersed in an isotonic solution of a non-electrolyte (e.g. sucrose) is greater than the electrolyte (e.g. KCl). According to Bennet-Clark this is “due to an electrical component (metabolically maintained) in water uptake and that the effect of the electrolytes changed ions was to either decrease or eliminate this component.”

Non-osmotic water absorption : A comparison of the osmotic potential (OP) of vacuolar sap determined by cryoscopy of expressed sap and by the method of plasmolysis, clearly indicates that the osmotic pressure determined by plasmolysis was often lower than that determined cryoscopically (Bennet-Clark, Greenwood and Barker 1936). From their observation it is clear that another force in addition to the osmotic pressure of the vacuolar sap and turgor pressure contribute to the absorption of water by cells. It is due to a ‘secretion force’ developed due to the existence of a mechanism pumping water actively into the vacuole, with expenditure of metabolic energy.

It is further noted that the water uptake by cells is somewhat related to respiration and this is taken as the non-osmotic water absorption of cells. It has been further observed that aerobic condition enhances water uptake by roots ; whereas the inhibition of respiration reduces the active transport of solutes into the vacuole, which in turn may affect the osmotic pressure of vacuolar sap and hence the absorption of water.

Further the addition of growth substances (e.g., IAA, NAA) stimulate absorption of water which clearly indicate that water absorption occurs actively. In case of parenchyma cells, this active water uptake is not at all significant. It has been suggested by

Thimann and Samuel (1955) that the main cause of water uptake by growth hormones, is due to increase in the extensibility of the cell walls, consequently reducing the turgor potential and decreasing the water potential of the cells.

Active water uptake therefore, has got no significant value in the water relation of parenchyma cells, although it may have some positive role in some specialised cells i.e., in water secreting glands (e.g., hydathodes) of some plants, in some "motor cells" in the upper surface of grass leaves and the pulvinus cells in the sensitive plant (*Mimosa pudica*).

Plasmolysis—It is the phenomenon of shrinkage of protoplasm

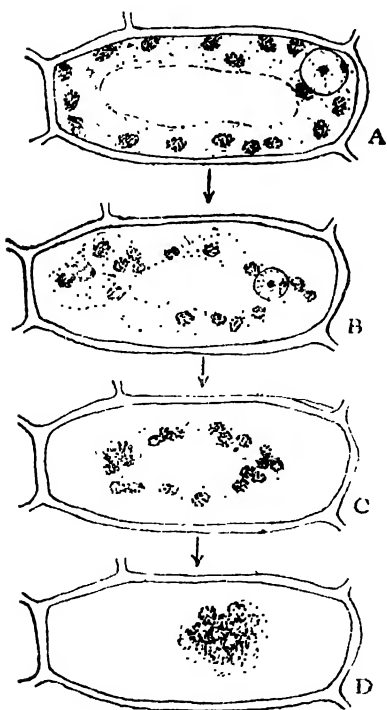


Fig. 3.10 A—D Showing the stages of plasmolysis. A—normal, B—incipient plasmolysis, C—further shrinking of protoplasm, D—complete plasmolysis.

of cell. If a turgid vacuolated cell containing sap which has certain osmotic concentration is immersed in a sugar or a salt solution of higher osmotic concentration (hypertonic concentration)¹ than that of the cell sap, then exosmosis² will take place and the hypertonic outer solution will try to become isotonic¹. Water will come out of the cell and there is a reduction of pressure (turgor pressure) upon the cell wall. If such a cell is examined under a microscope the characteristic shrinkage of the protoplasm can be seen. As the water will come out, the protoplasm will be found to separate gradually from the cell wall and form an irregular mass at the centre or in one corner of the cell (Fig. 3.10). This phenomenon of shrinkage of the protoplasm from the cell wall by the influence of certain hypertonic solution is known as **plasmolysis**. The stage at which the protoplasm just comes out from the cell wall is called an **incipient plasmolysis** or **limiting plasmolysis**.

Plasmolysis is easily observed

¹ A solution which has got the same osmotic pressure as the cell content is known as **isotonic solution**. A **hypotonic solution** on the other hand has relatively low concentration as compared to the cell content. A **hypertonic solution**, however, contains a higher concentration of solute particles than the protoplasm.

² The diffusion of the solvent from the living cell or structure due to its

in cells containing coloured plastids since the presence of colours makes the shrinking plastids easy to observe.

Plasmolysis is of manifold importance in cellular metabolism. First of all, it signifies the semipermeable nature of the cytoplasm. If it was not at all a semipermeable membrane, no plasmolysis could occur and the external solute particles would easily pass and enter the vacuole to make it in equilibrium. The approximate osmotic concentration of the cell sap and consequently the osmotic pressure can be determined by plasmolysis. Thirdly, it determines the living nature of the cell ; since no plasmolysis can occur in dead tissues due to absence of semipermeable cytoplasmic membrane.

If a slightly plasmolysed cell is immersed in pure water or in a hypotonic solution and since the cytoplasm is still acting as a semipermeable membrane, water will diffuse inwardly to the vacuole, the cell will gradually become turgid and recover its normal appearance. This recovery of turgidity is due to the endosmosis of water. This phenomenon is known as **deplasmolysis**. It proves the healthy nature of the cell.

Osmotic relation of a plant cell : The physical concept of osmosis can be correlated with a plant cell. The chief components of the plant cell involved in the osmotic process are : (a) the cell wall, a non-living structure possessing elasticity, almost completely permeable to vacuolar solutes ; (b) the outer and inner cytoplasmic membranes, the plasmalemma and the tonoplast—both partially semipermeable, allowing slow passage of sugars and inorganic ions ; and (c) the cell sap, an aqueous solution of sugars and mineral salts contained in the vacuole. With the above structure in mind we can consider three conditions :

(i) When the osmotic pressure of the cell sap (OP_c) is *greater* than the osmotic pressure of the external solution—(OP_s), water will enter the vacuole (endosmosis), with increase in the volume of the vacuole, the cytoplasm will be pressed against the cell wall, extending it. (The pressure exerted by the cell wall is called *wall pressure* (WP) and the pressure exerted on the wall—*turgor pressure* (TP). Wall pressure will be slightly less than turgor pressure until equilibrium is reached. When the state of equilibrium is reached, the cell will be in a state of turgor—the inward wall pressure restricting the intake of water.

The net force of the combined effect of the OP of the cell sap and of the forces restraining the wall expansion is known as *suction pressure* (SP) or diffusion pressure deficit (DPD).

(ii) When the osmotic pressure of the cell sap (OP_c) is *less* than the osmotic pressure of the external solution (OP_s) water will be

hypotonic nature, is called *exosmosis*. Conversely, the diffusion of solvent particles into a living cell or structure because of its hypertonic nature is called *endosmosis*.

forced out of the cells (exosmosis), resulting in decrease in vacuolar volume, rise in osmotic pressure of the cell sap and decrease in cell volume due to contraction of the cell wall through decreased turgor pressure.

A stage will be reached when turgor pressure equals wall pressure ($TP=WP=O$) and the cytoplasm just retracts from the cell wall. On reaching a state of the equilibrium i.e. when $DPD=O$.

$DPD=(OP_c-OP_s)+WP=O$, but since $WP=O$ the relation works out to $OP_c=OP_s$.

(iii) The osmotic pressure of the cell sap is *equal* to the osmotic pressure of the external solution i.e. the external solution is isotonic and the cell is in the first state of plasmolysis—*limiting plasmolysis*. If the external solution still remains hypertonic, water will be drawn further from the vacuole, the plasmalema will detach itself from the cell wall at the corners—this condition is known as *incipient plasmolysis*. Further, exosmosis often results in death of the cell possibly as a result of damage to the cytoplasm when it is pulled away from the wall. This extreme condition is characterised by rapid diffusion of vacuolar solutes from the cell.

Thus, if we represent osmotic pressure of the cell as OP , its turgor pressure as TP and suction pressure by SP , the relationship between the various forces will be

$$SP=OP-TP$$

$$TP=OP-SP$$

$$OP=TP+SP$$

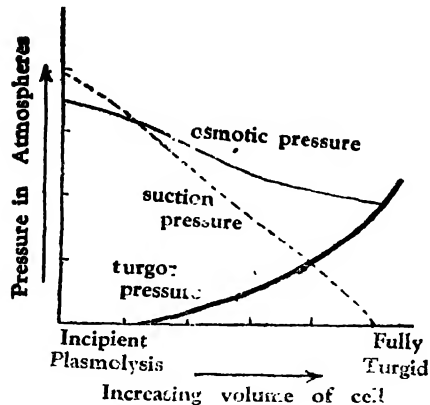


Fig. 3.11 Interrelationship among the OP , SP and TP of plant cells.

During deplasmolysis the value of TP being zero, suction pressure equals osmotic pressure i.e., $SP=OP$ and it decreases as OP decreases. But as the absorption of water takes place, the turgor has been regained, the value of OP falls due to dilution of the cell sap and the value of TP increases until $OP=TP$. At this point the value of SP is zero. At this stage the number of water molecules

moving into and out of the cell is almost equal, so no further absorption of water takes place. The cell has attained its maximum volume, as it is in a fully turgid state. The whole interrelationship among the OP , SP and TP is shown in the diagram (Fig. 3.11).

It is evident, therefore, from the above discussion that the suction pressure which forces water into the cell depends on OP and TP , as $SP=OP-TP$ and not on the absolute value of the OP of the cell.

Thus water can enter from a cell with higher osmotic concentration to a cell with lower osmotic concentration, provided TP of the former

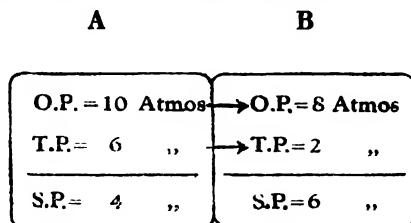


Fig. 3.12 Two adjacent cells showing the effect of suction pressure on the movement of water.

is much higher than that of the latter, so that the ultimate value of the latter is greater than the former.

The whole discussion of OP, SP and TP has been collectively termed as osmotic quantities of the plant cell (Fig. 3.12).

DETERMINATION OF DIFFUSION-PRESSURE DEFICIT (DPD) OR SUCTION PRESSURE (SP) OF THE CELL—The DPD is the result of the net force acting on water in the plant cells and is dependent on the osmotic pressure of the contents, the extensibility of the cell wall and tissue tension. The osmotic pressure of a solution which does not cause any change in the cells is equal to the average DPD of the cells. This unaltered condition of the tissue involved may be demonstrated by measurement of its weight, volume or length.

The most widely used methods of determining DPD are the gravimetric, vapour pressure, refractometer and Chardakov techniques.

(i) *Gravimetric method*—This method is based on the determination of OP of a solution in which cells achieve equilibrium without changes in TP and weight (or volume). The principle can also be followed by measuring the length of tissues rather than weight or volume (Ursprung, 1923). When the tissues are immersed in a solution* with an OP identical to the DPD, it gives an equilibrium state. But this however, does not hold true in all cases as it gives an erroneous result as a result of partial infiltration of intercellular spaces in some tissues by the immersion solution.

(ii) *Vapour pressure method*—This is based on the equilibrium of plant tissue against the water potential of vapour over a solution (Archichovskij *et al*, 1931). Since the equilibration took place in constant temperature water bath, the vapour pressure within the plant material can be measured enclosed in an constant temperature chamber (Spanner, 1951). Brix and Kramer (1962) used a thermocouple since it acts as an electric hygrometer to measure vapour pressure of the air which is in equilibrium with plant tissue in a closed chamber. When a current is passed through a thermocouple with plant tissue, enough cooling results, which causes the condensation of water film on the junction. Thus when the current is turned off, a temperature difference between the wet and dry junction takes place. This results in current measurable with a galvanometer. The rate of evaporation of water depends on the vapour pressure of the air which is controlled by the DPD of the plant tissue.

This system is calibrated against solutions of known DPD so that estimates of DPD of plant tissue can be obtained from the galvanometer deflections.

(iii) *Refractometer method*—This method is based on placing the plant tissue in solutions of different OPs and determining the solution at which there is no change in concentration as measured with refractometer (Lemee and Laisne, 1951). Since the refractive index of a solution has a linear relation to concentration and a hyperbolic relation to volume the refractive index method is more sensitive to water loss in hypertonic solution than to water uptake in hypotonic solutions.

(iv) *Chardakov method*—As it requires a very simple apparatus and a short equilibrium time, this method is widely used over vapour equilibrium methods (Chardakov, 1953). Sucrose solutions of different concentrations (covering estimated tissue DPD) are placed in test tubes with one ml of control of each solution in another set of test tubes. The control solutions are coloured with methyl blue. Plant tissues whose DPD to be measured are placed in test solutions. After a considerable time the tissues are removed from the test solutions and a drop of coloured control solution is transferred to the test solution. If water is absorbed by the plant material, the concentration of the test solution will be increased and the methyl blue drop of control solution will go to the surface due to difference of specific gravity. If, however, water is lost, the test solution will be diluted and the control drop will sink to the bottom. In cases where no exchange of water takes place, no change of concentration will occur, the control drop will diffuse out to the test solution. This point is taken as tissue DPD which is equal to OP of the solution in which no exchange takes place.

SIGNIFICANCE OF OSMOSIS—Osmosis, with its related phenomena plays an important role in different physiological aspects of plant life. First and foremost is its role in the absorption of water by root hairs from soil. Further, it controls the cell to cell diffusion of water in roots and also the movement of water from the xylem vessels to the neighbouring living cells and cells of the mesophyll in the leaf.

Osmosis makes the cells turgid and turgidity plays an important role in the enlargement of meristematic tissues, specially in the growth of root and shoot apices. Turgidity also helps to keep plant organs erect and leaves extended.

Many of the plant movements (e.g., turgor movement) which are concerned with the opening and closing of the flowers and also the autonomous movement of the lateral leaflets of Telegraph plant (*Desmodium gyrans*) and induced seismonastic movement of the leaflets of certain plants (eg. *Mimosa pudica*) are purely osmotic phenomena.

Osmosis is essential in the movement of the guard cells and it thus helps in the opening and closing of stomata. Osmosis has got an indirect control in the debiscence of the sporangia and also in the explosive bursting of the fruits of many plants. Osmotic concentration of the cell sap also plays an important role in the determination of the resistance to salinity, drought and frost.

3.4 Experimental work :

(a) IMBIBITION :

(i) Fill a thin glass bottle almost full with dry pea seeds. Add a little water to the bottle and seal the bottle with paraffin. Within a few hours the seeds will swell and almost fill the bottle. If the bottle is kept overnight as it is, the bottle is found to burst as a result of the swelling of the seeds due to imbibition.

(ii) Take a known amount of gelatin block (about 5 sq cm block), measure accurately the block on a graph paper. Place the block in a vessel containing water. After 1 hour take it up and wipe the superficial water on a blotting paper and measure again. Increase in the measurement clearly indicates the swelling of the block is due to imbibition.

(iii) That due to imbibition a pressure is exerted can be shown in this experiment. Some dry seeds with small quantity of water are taken in a glass jar which is covered by means of a flat disc. A pointer is attached at right angle to the vertical rod connecting the disc. It moves up and down along a graduated curved scale fixed with the apparatus (Fig. 3.13).

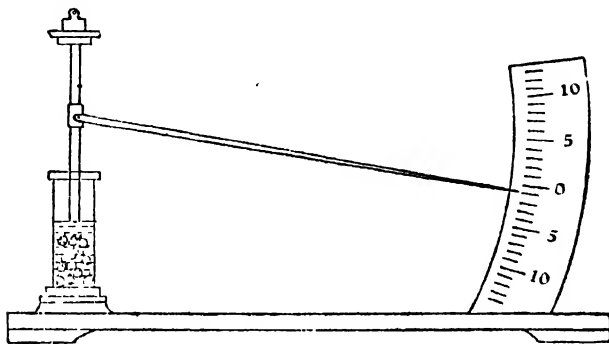


Fig. 3.13 An apparatus to measure imbibitional pressure in seeds.

Set up the apparatus in such a way that the pointer is fixed at zero position on the scale. Now as the seeds swell, they exert a pressure on the disc which moves the pointer downward on the scale, indicating imbibitional force of the swelling seeds.

(b) DIFFUSION :

(i) Take a beaker almost filled up with water. Now drop some pieces of copper sulphate or potassium permanganate crystal into the water of the beaker

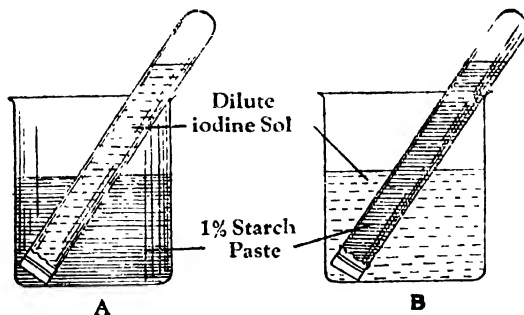


Fig. 3.14 Diffusion through a semipermeable membrane. Molecules of iodine solution pass through the membrane ; starch does not.

and leave them undisturbed. (To do so, insert some dry piece of above chemicals into a glass tube. Hold the mouth of the tube with finger and then insert it to the water of the beaker and then release the finger. The chemicals will fall to

the bottom). The molecules of the chemicals will move gradually from higher concentration to lower and will be completely distributed within the solvent after a few hours.

(ii) Take some dilute iodine solution in a test tube, cover its mouth with a semipermeable membrane, invert the test tube in a beaker containing 1% starch paste. Take another test tube and this time pour some starch paste and fasten its mouth with a semipermeable membrane. Now invert the test tube in another beaker containing a dilute solution of iodine (Fig. 3.14).

After about an hour the characteristic starch-iodine colour (blue) appears in the starch paste but not in the iodine solution. This clearly indicates that the molecules of the iodine solution pass easily through the membrane in either direction, but starch does not.

(c) OSMOSIS :

(i) *Osmosis as a physical process*—Take a thistle funnel and close its broad mouth with a piece of parchment paper. Invert it and insert the mouth of the funnel in a beaker containing water. Now fill the funnel with a strong sugar solution (10-20%). Mark the level of the sugar solution in the narrow tube. After a few hours the level of the sugar solution rises in the tube (Fig. 3.15) due

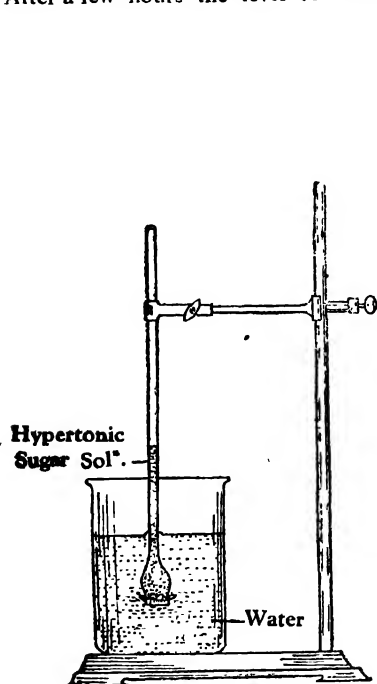


Fig. 3.15 An apparatus demonstrating the physical process of osmosis.

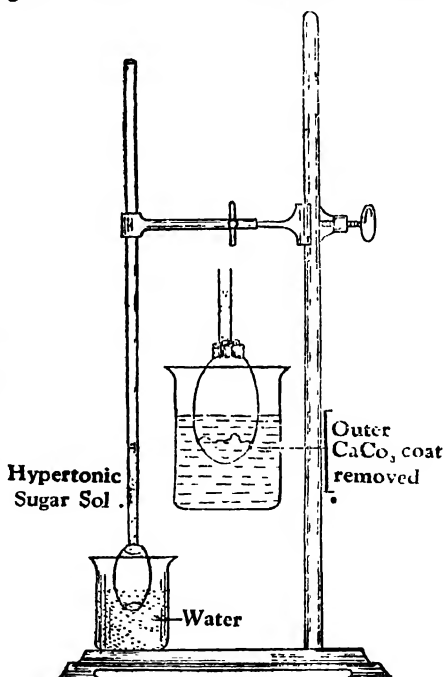


Fig. 3.16 Egg osmoscope.

to the accumulation of the water molecules from the beaker through the membrane (endosmosis). Now test the water of the beaker for sugar (refer article 1.15A tests for carbohydrate). Positive reaction for sugar indicates that some sugar solution has come out through the membrane (exosmosis) as the membrane is not semipermeable but differentially permeable.

(ii) *Osmosis through semipermeable membrane of an egg (egg osmoscope)*—Make a small hole at one end of an egg and carefully remove all its inner contents. Now dissolve away the calcareous shell with dil. HCl to bring out the thin inner membrane. This is a semipermeable membrane (allows only water to pass). Wash the egg and the membrane with water and insert a narrow glass tube through the hole of the egg and seal it with sealing materials. Now pour some sugar solution (10-20%) through the tube to fill the membraneous sac with it. Add further sugar solution to raise its level upto certain height in the glass tube. Mark the level and then place the egg deep within a beaker containing water. After sometime the level of the sugar solution in the tube is seen to rise due to endosmosis through the membrane (Fig. 3.16).

(iii) *Osmosis through potato (potato osmoscope)*—A small block of potato is made from a potato tuber (after removing its skin). Now scoop out carefully the central region of the block with the help of a scalpel to form a deep hollow cavity (care should be taken not to pierce the side or bottom of the block with scalpel). The central hollow cavity is now filled up partly with 10-20% sugar solution.

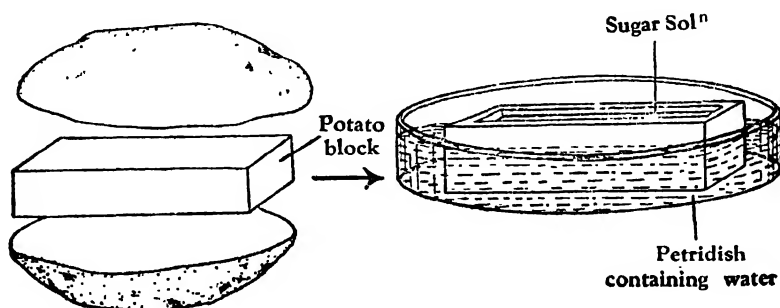


Fig. 3.17 Potato osmoscope.

Mark the level of the sugar within the cup with a pin. Now place the cup in a petridish containing water (level of water should be below the rim of the cup) which is coloured red with eosin (Fig. 3.17). After a few hours the level of the solution in the cup is seen to rise due to diffusion of water molecules from the petridish through the semipermeable membrane.

(iv) *Plasmolysis*—Peel off a thin strip from the lower surface of a *Rhoeo discolor* leaf and observe under a microscope. Note the turgid cells with coloured cell sap. Now a strong solution (0.5M-1M) of sugar is added through the sides of the cover slip. After a few minutes note down the effect of this solution on the cell sap. The coloured protoplasm is found to have partly shrunk from the cell wall (incipient plasmolysis) which will ultimately come to the centre of the cell (complete plasmolysis).

(v) *Measurement of OP in living cells*—Prepare a number of different concentration of molar solutions (0.05M to 0.25M) of sugar from a stock solution (Refer 1.9 (b) and keep the solutions in separate petridishes. Now peel off some thin strips from the lower epidermis of a *Rhoeo discolor* leaf and immerse one small strip in each of these solutions. After an hour examine each strip under microscope; which will show, some in which all the cells are plasmolysed, some in which all the cells are turgid and some in which 50% of the cells are just beginning to show signs of plasmolysis (incipient plasmolysis). This solution at incipient plasmolysis is isotonic and its concentration is approximately equal to the concentration of the cell sap. Then the corresponding OP of the cell sap can be easily calculated by the formula

$$OP = CRT$$

Where OP is the osmotic pressure ; C stands for the concentration of the cell sap ; R is a gas constant (0.082) and T is the absolute temperature ($273 + \text{room temperature}$).

3.5 Energy in the cell : All living cells require energy for their activities. Supply of energy is, therefore, important to the cell. The ultimate source of energy in biological system is light. When sunlight falls on the green leaves, the radiant energy is trapped by the green pigments of the cells. The cells then store this energy in carbon-to-hydrogen (C—H) and in carbon-to-carbon (C—C) bonds of glucose and other organic substances during photosynthesis. Within the cell these organic compounds are oxidised in small steps during respiration, thus breaking down the C—H or C—C bonds of glucose which liberates ultimately a large amount of energy. The energy that is liberated during respiration is utilized in various metabolic functioning of the cells. But since the use of this energy is not immediate, the energy evolved in respiration from glucose is immediately stored in some high-energy phosphate compound like adenosine triphosphate (ATP.), the triphosphates of uridine, cytidine and guanosine (UTP, CTP and GTP), phosphocreatine, phosphoenol pyruvic acid and amino acid adenylates and uridine diphosphate glucose from which a small fraction of the energy can be utilized when required. The usable energy (ΔF) values are obtained from the amount of high-energy compound that participate in a reaction i.e., ΔF may be defined as the measure of differences between the free energies of reactants and of products. If the energy product is higher, energy must be supplied in the reaction to proceed. The "high-energy" compounds are unique : in the difference between the compounds and the products of their hydrolysis, in their ionization, in their resonance stabilities and in the intramolecular electrostatic repulsions.

The most important feature of the high energy compounds is that they are anhydrides of phosphoric acid with either a second phosphoric acid to form the nucleoside di- or triphosphates or with a carboxylic acid (i.e., acetic acid), to form acetyl phosphate. In some cases phosphoric acid combines with a basic nitrogen compound as in phosphocreatine. There anhydride bond reduces the resonating groups in the molecule. The stability of a compound depends upon the number of resonating forms and since the high energy compounds contain less resonating groups, they are less stable and on hydrolysis therefore, yield a large amount of energy.

Adenosine triphosphate is of fundamental importance in biological processes. It is present in almost all living organisms. Its main role in the energy relation of the cell has been explained by Fritz Lipmann (1941).

ATP is not so complicated in structure as some other organic molecules are. It consists of a nucleotide, adenosine (represented by A)

with which is attached three phosphate radicals (represented by P). The structure of ATP can be represented as

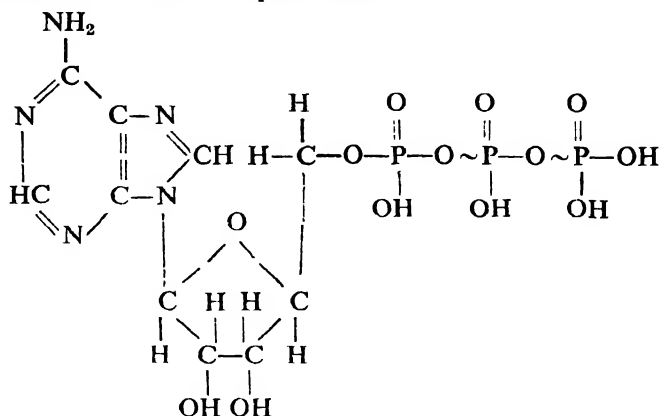
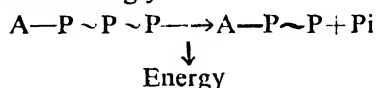


Fig. 3.18 The structure of adenosine triphosphate (ATP) molecule.

The presence of the phosphate groups has a special significance and found to be attached in two distinct energy levels; the energy level which is usually represented by ordinary chemical bond (—P) and a high energy level bond represented by ($\sim\text{P}$). It means, therefore, that much energy will be required to form the bond and consequently much energy will be released (about 12×10^3 cal or 12 Kcal) when this bond is broken. To get energy, therefore, one of the high energy phosphate bonds ($\sim\text{P}$) should be removed, the result is the formation of a substance with only two phosphate groups—known as adenosine diphosphate (ADP). The conversion of ATP to ADP takes place accordingly.



Now, the supply of ATP in a living cell is limited. It will use up all its available ATP within a very short period and until and

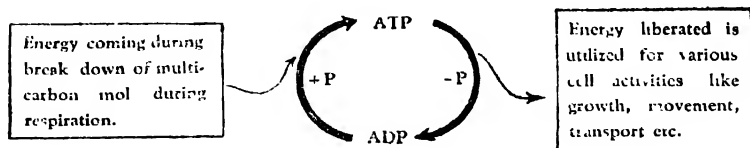


Fig. 3.19 ATP-ADP cycle showing the energy transformation in living cell.

unless the ATP is regenerated in the living cell the metabolic activities of the cell cannot take place normally. The ATP again can be regenerated by putting a phosphate group to the ADP molecule.

The whole cycle of the energy relation in the cell is represented in Fig. 3.19.

Similarly, the other nucleoside diphosphate like guanosine (GDP), cytidine (CDP) and uridine (UDP) can be phosphorylated by ATP molecules to give rise to their corresponding triphosphates. ATP is involved in fat, carbohydrate and protein synthesis, UTP in glycogen synthesis, GTP in carbohydrate and protein and CTP in phospholipid synthesis.

All these energy transformations are always taking place within some tiny particles of the cell known as mitochondria, the "power-house" of the cell. It is here that the breakdown of carbon atom (from glucose, etc.) in respiration helps to release energy which is built into ATP molecules. From the mitochondria the molecule of ATP diffuses into the cytoplasm where it helps to release free energy utilized in different cell activities. Release of the energy from ATP means the formation of ADP which returns to the mitochondria where the resynthesis of ATP molecule takes place.

3.6 Control of cellular metabolism : The main controlling system in the normal life and activities of the cell is the nucleus. Within the nucleus, chromosomes which are formed largely with deoxyribonucleoprotein are the fundamental body of control. This deoxyribonucleoprotein consists mainly of protein and deoxyribonucleic acid which is also abbreviated as DNA.

This DNA is one of the most vital substances in the cell as it is the main hereditary material of life. It controls the entire range of activities within the cell. DNA mainly controls the synthesis of certain specific types of ribonucleic acid (RNA) which then moves out of the nucleus and then to the cytoplasm, finally associated with the ribosomes. These RNA then direct the synthesis of specific types of protein (refer *role of nucleic acid in protein synthesis* in article 10.6) and also of enzymes. It is the enzymes that determine the types of chemical reactions that should proceed within the cell and which consequently determine the metabolic and morphologic features of the cell.

SELECTED QUESTIONS

1. Describe what you know about the modern concept of a plant cell from the physiological point of view.

Refer article 3.2

2. Describe the sub-cellular particles in a cell particularly in relation to their physiological activities.

Refer article 3.2

3. What do you know about the energy in the cell.

Refer article 3.5

4. Explain osmosis and osmotic pressure. Describe how these are related to life of plant.

For the first part refer topic *osmosis* and for the last part refer *significance of osmosis* in article 3.3(iii)

5. How would you measure osmotic pressure of plant cells ?

Refer topic *methods of measuring osmotic concentration of cell* in article 3.3(iii)

6. Distinguish between osmosis and diffusion. Discuss their nature and function.

Refer articles 3.3 (ii) and 3.3(iii)

7. What do you understand by diffusion pressure, turgor pressure, suction pressure and osmotic pressure. Discuss the relationship among them.

Refer articles 3.3(ii) and 3.3(iii) and topic *osmotic relation in plant cell* in article 3.3(iii)

8. Distinguish between osmotic pressure and suction pressure. How do they influence water absorption in a meristematic plant cell.

For first part refer topic *osmotic relation in plant cell* in article 3.3(iii)

For second part refer topic *active absorption* in article 4.5

9. Define osmosis. How it is related to the living processes of plant ? Illustrate your answer by describing the mechanism of absorption of water and solutes in plants.

Refer topics *osmosis* and *significance of osmosis* in article 3.3(iii)

For the last part refer topic *active absorption* in article 4.5 of Chapter 4

10. Explain briefly plasmolysis in plant cell. What light does it throw on the physiology of the cell ?

Refer topic *plasmolysis* in article 3.3(iii)

11. Explain the phenomenon of plasmolysis. How can you make use of this in determining OP of cell sap ?

Refer topic *plasmolysis* in article 3.3(iii) and for the last part refer topic *methods of measuring osmotic concentration* in article 3.3(iii)

12. Write what you know about the control of cellular metabolism.

Refer article 3.6

13. How do you determine osmotic pressure in plants ? Discuss its importance in passive and active absorption of water by cells.

For first part refer *methods of measuring osmotic concentration* in article 3.3(iii)

For second part refer article 4.5 in Chapter 4

14. Discuss the significance of suction pressure and turgor pressure in the water relation of a plant. How suction pressure of cells is measured ?

Refer *osmotic relation in a plant cell* under article 3.3

Absorption of Water and Mineral salts

For majority of the land plants, soil is by far the most important substratum which influences the growth and development. It is the most complex and dynamic medium for growth of the plants. For almost all terrestrial plants, the main source of water and mineral substances is the soil, which are absorbed by the root system. Only a negligible fraction of the total water absorbed takes place through other organs. A thorough understanding of the structure and properties of the soil is, therefore, necessary to understand the mechanism of water absorption by land plants.

The soil¹, considered as a part of the earth's crust, is formed by the mechanical disintegration and chemical decomposition of rocks over a long period of time. The weathering of rocks may be either (a) physical—through the agency of heat, water, wind, plants and animals or (b) chemical—by solution, hydrolysis, carbonization, oxidation and reduction.

4.1 Components of the soil: Soil, thus formed, generally consists of five different components: (i) **mineral materials** of various sizes; (ii) **organic matters** derived by the decomposition of plant and animal bodies; (iii) **soil organisms** of various kinds including bacteria, fungi, certain algae, worms, insects etc.; (iv) **soil solution** containing mainly inorganic substances in aqueous form, generally as a film of water surrounding the soil particles and (v) **soil air** containing oxygen, nitrogen, carbon dioxide and a trace of other atmospheric gases.

(i) **MINERAL MATERIALS OR ROCK PARTICLES:** The rock particles from which ultimately the soil produced by the various weathering agencies vary greatly in size and can be classified on the basis of size (diameter) of the particles. If the particles are coarse in texture, having a diameter about 2.00 mm and upwards, the soil is said to be *gravel*. If the particles lie between 2.00 mm and 0.02 mm in diameter, they are called *sand*. If the particles are very fine having a diameter less than 0.002 mm these are known as *clay*. When the particles have an intermediate size i.e., between 0.02 mm and 0.002 mm, the soil is said to be *silt*.

¹ According to Buckman and Brady (1960), "the soil may be defined as a natural body, synthesized in profile form from a variable mixture of broken and weathered minerals and decaying organic matter which covers the earth in a thin layer and which supplies, when containing the proper amounts of air and water, mechanical support and in part sustenance for plants."

The classification of various soil separates together with the specific diameter limits is given in the following table.

TABLE 2

Diameter limits (in mm)	Types of soil separate	Percentage found in a typical		
		Sandy loam	Clay loam	Clay
Above 5.00	Coarse gravel	—	—	—
2.00 - 5.00	Fine gravel	—	—	—
0.20 - 2.00	Coarse sand	65	30	1
0.02 - 0.20	Fine sand	20	30	9
0.002 - 0.02	Silt	5	20	25
Below 0.002	Clay	10	20	65

According to the abundance of different particles varying in size and shape, the soils can be grouped into three broad textural classes :

(i) *sandy*—which consist mainly of sand particles (70% by weight)
(ii) *clayey*—those which consist mainly of clay particles (40% and above). A soil with equal proportion of sand, silt and clay is called
(iii) *loam*—the most suitable soil for plant growth. A loam soil when predominated by sand particles is called *sandy loam* and if clay predominates it is called *clay loam*.

(ii) **ORGANIC MATTER** : In addition to mineral matters of variable sizes, the soil contains a considerable amount of organic matter formed by the gradual decomposition of the plant and animal remains. The partially decomposed dark coloured, homogeneous, amorphous, partially odourless, complex colloidal substance is called *humus*. The proportion of organic matter in the soil varies from 1 percent or less in case of desert soil to about 80 percent in case of a bog soil.

The dark color of the soil clearly indicates the proportion of humus in the soil. The forest soil is very rich in humus because of the decomposition of the leaves and the other plant parts easily by micro-organisms.

When the organic matter of the soil is coupled with the clay materials it produces a "colloidal complex" which according to Waksman (1936) plays an important role in the dynamic activities of the plant. Since the addition of humus to the soil tends to bind the soil particles together, it reduces the pore size of the soil particles. Consequently, the water holding capacity of this type of soil will be greater than the pure sandy soil. So the movement of air and water through this type of soil will be reduced to a great extent. It not only binds the sandy soil but also opens the clay soil to increase percolation and aeration.

The important nutrients (e.g. nitrate, potassium, calcium, phosphate etc.) of the plants are found to have been derived partly from the humus and partly from the breakdown of the mineral

elements of the soils. Many of the other soil properties are generally influenced by the colloidal complex.

(iii) **SOIL ORGANISMS** : Some of the living organisms of the soil play a significant role in determining the nature of the soil. In fact, plants and animals play an important role, particularly in the development and formation of soil. Practically *no biological importance will exist in the soil if it has got no micro-organisms*. Almost all the major groups of micro-organisms are present in the soil, although in different proportions. These organisms are always present in a colonial form rather than evenly distributed throughout the soil.

Among the micro-organisms most abundant in the soil are bacteria, soil fungi, soil algae etc. Bacteria are most abundant among the living organisms present in the grassland soil. Many kinds of bacteria are found to be present in the soil. They may be aerobic or anaerobic in nature. Among the aerobic bacteria may be mentioned the name of nitrogen-fixing bacteria and cellulose-decomposing bacteria. The frequency of the bacteria is more in the upper strata of the soil than in the lower soil strata, where the number of the bacteria decreases gradually with depth. The most important anaerobic bacteria is *Clostridium tetani*, which thrives well when the aeration of the soil is minimum.

Besides true bacteria, a number of actinomycetes are found in the soil.

Fungi are another kind of decomposers in the forest soil which produce an irregular net work of filament on the upper surface of the soil. These fungi are strictly speaking not micro-organisms. They usually bring about the decomposition of cellulose, pectin and chitin.

Approximately 55 or more different species of algae have been found in soils. The three major groups of algae which are usually present abundantly in the soil are Cyanophyceae, Chlorophyceae and Bacillariophyceae.

Among the soil fauna which can also contribute towards the soil structure are, earthworms, protozoa, nematodes, insects especially in larval stages and a number of animal species which burrow through the soil.

(iv) **SOIL SOLUTION** : Soil is the main source of water for plants, although the amount present varies greatly according to the nature of the soil as well as under different conditions. The soil particles always retain a thin film of water and a variety of organic and inorganic materials in aqueous form surround the soil particles. This aqueous solution is generally known as *soil solution*.

The concentration of this soil solution largely depends on the amount of water present in the soil.

The activity of the soil micro-organisms is largely dependant on the water content of the soil as well as the soil solution, as the main

nutrient substances necessary for normal growth of the micro-organisms remain in the soil solution.

A solid substance remains in the soil in the form of a compound, which when dissolved is always split up into its component ions. As for example, a molecule of sodium chloride (NaCl), is split up into sodium (Na^+) and chlorine (Cl^-) ions in the water. Water itself may also be split off into hydrogen (H^+) and hydroxyl (OH^-) ions. Normally, when water is ionised, the amount of hydrogen and hydroxyl ions remain the same. In some cases, however, these ions may be added in the soil water from other sources. If in any soil the number of hydrogen ions is greater than the hydroxyl ions we call it as an *acid soil*. If hydroxyl ions outnumber the hydrogen ions, we call it as *alkaline* or *basic soil*. The acidity and alkalinity of the soil are important factors in the development of the plants as well as the micro-organisms.

(v) **SOIL AIR** : Since a great variation exists in the shape and size of the soil particles, it indicates that even the tightly packed soil contains a number of intercellular spaces between them. These tiny pockets are usually filled up with gases, mostly the gases of the atmosphere—air. This is known as *soil air*. Compared with the atmospheric air, the soil air contains more CO_2 and less O_2 and more moisture. Under normal condition the intercellular spaces (containing air) are mixed up with soil water. In the desiccated soil, it is filled entirely with air, whereas in case of water logged soil with soil water. If the pore space is of normal size, normal growth of the root system takes place ; if however, the pore space is too large, water and other aqueous solutions will drain out easily. If it is too small, the water will be retained in large amounts. In both the cases the normal growth of the root system will be disturbed. The soil air is, therefore, essential for normal growth and development of the plants.

4.2 Types of water in the soil and their availability and usefulness for the plants : Majority of the plants growing under terrestrial environment, rooted in the soil, obtain almost all of their requirement of water and mineral substances from the soil. The main source of this soil-water is rainfall. Of a heavy rain that falls upon the surface of the soil, a part runs off immediately, a part percolates through the soil and another portion is lost by evaporation. The part of the water which runs off is known as *run-away water* and is not available to the plants for absorption. The portion of the water which percolates through the soil fills the spaces between the soil particles—this is known as *pore space* which varies with the type of the soil. The water held in the soil can be classified into four categories.

(i) **GRAVITATIONAL WATER** : When the rain ceases or if the soil is well irrigated, a certain amount of water drains off immediately due to gravity. The flow of this water is manly dependent on the pore space of the soil. This water is known as *gravitational water*

which is of little use to the plant, as it moves rapidly below the reach of the root system. If it remains indefinitely, the soil is said to be waterlogged and no plants can grow because of aeration. Some species e.g. *Oryza sativa*, however, can grow well under these conditions probably because the roots are efficiently aerated via the shoots. Submerged parts of many aquatic plants are also supplied with oxygen in this way.

(ii) **CAPILLARY WATER** : When the water is trickling downwards due to gravity, a portion of the water is retained around and between the soil particles due to surface tension. This water is known as *capillary water* and is of prime importance as it is this water which is available to the plants by the root system.

(iii) **HYGROSCOPIC WATER OR IMBIBED WATER** : Due to continuous evaporation of water from the upper layers of the soil, the percentage of capillary water gradually decreases. As a result of this decrease, the molecular attraction between the soil particles and water particles increases and ultimately occurs as an extremely thin film (about 4.5μ thick) on the soil particles. This water is known as *hygroscopic water* and is not available to the plants under normal condition ; although certain plants can absorb this water through special type of hygroscopic root system.

The molecular attraction (adsorption) of this water with the soil particles is so high that the loss of this water to the atmosphere is practically impossible under normal condition, which, however, can be evaporated by heating the soil at high temperature.

(iv) **COMBINED WATER** : A small portion of the soil water is chemically bound with the soil elements and is known as *combined water*. After heating the soil at high temperature (bright red heat) all the combined water can be eliminated from the soil leaving aside the hydrated oxide of certain metals. This water is practically unavailable to the plants.

4.3 Water holding power : The total amount of capillary water, hygroscopic water, combined water and the water vapour together constitutes the **field capacity** or the **water holding capacity** of the soil and it is the maximum water that the soil can hold after the gravitational water has drained away. Field capacity, however, varies considerably with the types of soils and *soil profile*¹ (or *soil horizons*²). The soil can attain its field capacity within a very short period provided the *water table* (the level at which soil is saturated with water) is not far below the soil surface.

¹ *Soil profile* : "A vertical cross section of the soil from the surface into the underlying unweathered material".

² *Soil horizon* : "A layer of soil approximately parallel to the land surface with more or less well defined characteristics, that have been produced through the operation of soil building processes. Each layer differs from the one above or below in some characteristic. The result of soil forming processes working for long periods of time is the gradual differentiation of layers or horizons within the parent material. Collectively, these horizons are called a *profile*".

The supply of water to the plant is dependent on the field capacity of the soil. Due to continuous absorption of water by the plant, the amount of water present in the capillary spaces is greatly reduced. Below certain level of moisture content of the soil, plants tend to wilt permanently—when the soil particles still retain certain amount of water in the soil. If plants still absorb water, the capillary water further decreases and a point is reached when the plant cannot recover from the wilting condition (permanent wilting). It can, however, be recovered by the addition of more water to the soil. The moisture left in the soil expressed as, *percentage of the dry weight of the soil at which the plants are permanently wilted, is known as permanent wilting percentage or simply wilting coefficient*.

The wilting coefficient is one of the important characteristics of the soil.

It is evident, therefore, from the foregoing discussion that the amount of water between full field capacity (which represents the maximum water limit) and wilting coefficient (represents the minimum water limit) makes up the *available water*. A small fraction of the capillary water (which, however, remains at wilting coefficient stage), hygroscopic and combined water as well as water vapour can not be utilized by plants. This water is known as *non-available water*.

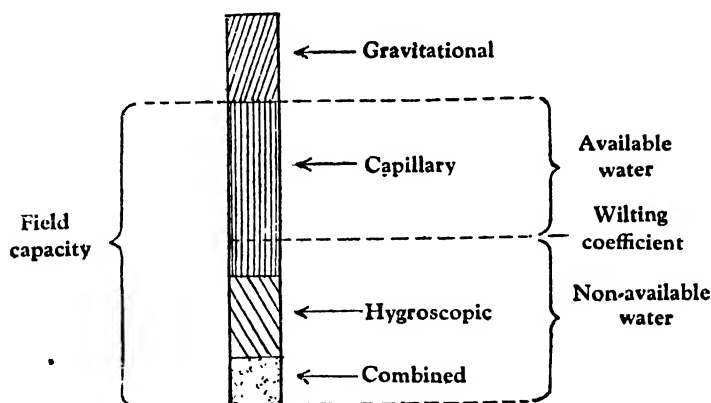


Fig 4.1 Generalized diagram showing the types of soil water and their availability to the plants. The relative proportions and the value of wilting coefficient differ according to the nature of the soil.

A schematic representation of the soil-water relation is given in Fig. 4.1.

Total soil-moisture stress (TSMS) represent the mean potential of water in soil resulting from all the factors which affect it (Wadleigh and Ayers, 1945).

4.4 Measurement of soil water : The various methods of determining the amount of water present in the soil are important in

elucidating the water relation of soils. Some of the methods for determining various soil water relations are given below :

(a) **WATER CONTENT OF SOIL**—It means the amount of water actually present in the soil at any particular time and is usually expressed as a percentage of water present.

Collect about 50 g of soil in a container from a field and take the weight. Dry the soil to a constant weight in an oven at a temperature of 105°C for approximately 24 hours. The loss in the weight will determine the amount of water which was present in the soil and the percentage of the water content can be calculated from the following formula

$$\text{per cent water content} = \frac{\text{loss in weight}}{\text{dry weight of the soil}} \times 100$$

Loss in weight can be determined by subtracting the final weight after drying from the initial weight with the container plus soil before drying. Whereas the dry weight of the soil can be determined by subtracting the weight of the container from the total weight of the container plus soil after drying.

(b) **WATER HOLDING CAPACITY OR FIELD CAPACITY**—It is a measure of the amount of water present in a given soil when it is saturated. The water holding capacity generally depends on the nature of the soil particles. Thus clay can hold more water than sand.

To find out the water holding capacity, the container with its soil (obtained after drying in the first experiment) is covered with a screen (only to prevent the loss of soil from the top) and immersed in water at least for overnight. Then next morning suspend the container to drain off the water for 30 minutes ; wipe off the superficial water on the outside of the container and reweigh. The percentage of water holding capacity can be calculated from the formula

$$\text{water holding capacity (\%)} = \frac{\text{gain in weight}}{\text{dry weight}} \times 100$$

Gain in weight can be determined by subtracting the dry weight with container in the first experiment from the weight after soaking and draining the water. Dry weight of the soil can be determined from the first experiment.

(c) **PERMANENT WILTING PERCENTAGE**—It is one of the most important properties of the soil, since it indicates the amount of water in the soil which is actually available to the plant. Different soils have different wilting percentage and therefore affect growth of the plant. It may be defined as the percentage of water present in the soil after a plant has wilted.

To determine the wilting percentage, take a well grown potted plant and cover the pot with a plastic bag to prevent loss of water from the soil surface. Weigh the whole pot and keep it as it is, when the soil will gradually dry up and the plant tends to wilt. At the

permanent wilting condition (i.e. when the plant will not recover after being placed overnight in high humidity chamber) take the weight of the whole pot again. Using the same procedure to determine the dry weight of the soil as in the previous experiment the percentage of the wilting capacity can be calculated as follows

$$\text{permanent wilting (\%)} = \frac{\text{loss in weight}}{\text{dry weight}} \times 100$$

4.5 Absorption of water by land plants : Water plays an important role in the life of plants. Majority of land plants take their necessary amount of water mainly from the soil. When water falls on the surface of the soil, some amount of it percolates down through the soil forming free or gravitational water, while some of it is retained by the soil particles as a thin film surrounding it, this is known as *capillary water*. This capillary water is actually available to the plants from the soil for absorption. Entry of water generally takes place through root hairs and epidermal cell of the roots (which remain in contact with the soil particles surrounded by a film of water) and then by crossing the cortex, endodermis and pericycle it reaches the xylem of roots.

There are two main types of water absorption by land plant viz. (i) **passive absorption** and (ii) **active absorption**.

(i) **PASSIVE WATER ABSORPTION :** In the mesophyll cells of the leaves, the diffusion pressure deficit (DPD) of water increases as evaporation takes place from the cell wall into the intercellular spaces. As a result, movement of water from the vacuole into the protoplasmic region and then from protoplasmic layer to the cell wall occurs. This increased DPD is generally transmitted to all parts of the cell. Consequently, the water in the xylem vessels remains in a state of tension. According to most authors, water in the cells of the absorbing region of the root generally remains in a state of much tension, thereby increasing more DPD in the peripheral cell walls of young roots than other regions. DPD is increased due to the amount of negative tension to which it is subjected $DPD = OP - (-TP)$. Movement of water takes place from the soil into the root as soon as the DPD of water in the peripheral walls of the young roots exceed that of surrounding water in the soil. This type of absorption is called "passive absorption" as the topmost region of the plants plays a major role in the entrance of water into the roots and the roots are found to be playing a subsidiary role. Since the water uptake takes place due to the activity of the shoot, the shoot can absorb water through dead roots and even can absorb it at faster rate (Kramer, 1959).

(ii) **ACTIVE WATER ABSORPTION :** Here the water is absorbed and moved in an upward direction through plant body as a result of some mechanism that takes place in the root cells—this type of water absorption in which the mechanism is localised mainly in the root system is called "active absorption."

Relatively simple osmotic mechanism which may be involved in the active water absorption has been shown by Atkins (1916) and Priestley (1920-22). Though the intervening root cells have higher osmotic pressure than that of the external soil solution, still an osmotic movement of water from soil to xylem vessels generally takes place through the multicellular membrane of the intervening root cells. Root hairs become turgid as a result of absorption of capillary water by endosmosis. Then, osmosis is set up between cortical cells of the root and root hairs, the latter become flaccid owing to the absorption of water by cortical cells; the flaccid root hairs again become turgid by absorption of capillary water. In this way, transfer of water from the soil to the cortical cell goes on continuously. Simultaneously,

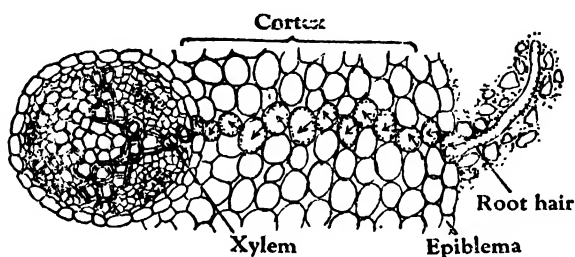


Fig. 4.2 Showing water absorption by root. Arrows indicate the path of water entry from root hair to xylem.

cell to cell osmosis of the cortical cells is set up. In this way, all the cells become turgid and the absorbed water is ultimately forced into the xylem vessels as no osmosis takes place between living cells and xylem vessels. From xylem vessels, water is conducted to other parts of the plant body (Fig. 4.2).

It has been found that though large amount of water exudes as a result of active absorption, in general, the amount of water moving into the plant body due to active absorption, is relatively smaller than the amount of water entering due to passive absorption.

4.6 Factors affecting absorption of water: Since the absorption of water is indirectly related with the transpiration of plants (refer *theory of passive water absorption* in article 4.5), therefore, any factor which influences the rate of transpiration is indirectly related to the absorption of water by land plants.

When the roots absorb all the available water surrounding the soil particles, soon the water becomes limiting and for further absorption of water, the roots, must elongate. Therefore, any factor which influences the growth of the roots will also indirectly affect the absorption of water.

The rate of absorption of water by land plants is influenced by a number of external and internal factors.

EXTERNAL FACTORS :

(i) *Water content of the soil or available soil water*—Generally, the rate of water absorption is influenced by the amount of water present in the soil. Large amount of water that is present in the soil enhances the rate of absorption while waterlogged soil retards it. In many soils, water though present in sufficient quantities is not absorbed by plants because of either the presence of toxic substances or very high osmotic concentration. Such soil is known as **physiologically dry soil**¹. Over a range of soil water content between the field capacity and the permanent wilting capacity, absorption of water takes place almost equally in case of light and medium textured soil. In heavier textured soil, the absorption of water is retarded in the lower part of this range.

(ii) *Soil temperature*—It is one of the most important factors which influence the rate of absorption of water by roots. It is evident that the rate of water absorption increases markedly with a rise in the soil temperature. At low temperature, however, the rate of absorption greatly slows down because :

(a) at low temperature, the viscosity of water increases and it slows down the rate of absorption :

(b) low temperature retards the growth of the roots which thus fail to encroach upon new soil particles to get more water ;

(c) at low temperature, the viscosity of the protoplasm and cell wall increases and consequently their permeability to water decreases thus lowering the rate of water absorption ; and

(d) low temperature decreases the metabolic activities of the root cells thus decreasing the energy of the cell which may be directly or indirectly required for water absorption by the plants.

(iii) *Oxygen of the soil air*—Generally, absorption of water by roots of most plants takes place rapidly in soils that are well aerated. Retardation in the rate of water absorption occurs in poorly aerated soils. Reduction of oxygen concentration in the soil causes a reduced rate of respiration which influences directly or indirectly the other metabolic activities of the cell. The consequence of such a reaction, is the reduced rate of water absorption. Low oxygen concentration, in some cases, causes the accumulation of large amount of carbon dioxide within the cell that produces toxic effect which may be responsible for decrease of water absorption. Further, increase in

¹ The decrease in the absorption of water may be due to actual shortage of water in the soil when the soil is said to be **physically dry soil** or it may be due to **physiological dryness of the soil**. The soil is physiologically dry when there is plenty of water in the soil but the soil contains an excess of soluble salts which make water absorption extremely difficult. Two extremely diverse groups of plants grow in the above two soil conditions. Although the exact relation is not known, it is of interest to note that the halophytes, living in the physiologically dry condition, exhibit succulence and heavy cutin ; typical xerophytes are familiar in the physically dry habitat.

carbon dioxide increases the viscosity of protoplasm and decreases permeability ; both of which would retard absorption.

(iv) *Concentration of the soil solution*—Absorption of water by the plants is usually inversely proportional to the concentration of the soil solution. It generally increases if there is decrease in the concentration of the soil solution ; on the other hand, the rate of absorption of water decreases with the increase in concentration of the soil solution. Alkali and saline soils are purely physiologically dry soils for the plant ; consequently no absorption of water generally takes place in these soils.

(v) *Acidity and alkalinity of the soil*—In most cases the rate of the absorption of water is greatly influenced by the pH of the soil solution. Some physiologists suggest that the rate of absorption of water decreases in an alkaline soil and increases in an acid soil.

INTERNAL FACTORS :

(i) *Root pressure*—It plays an important role, as the hydrostatic pressure set up in the roots helps in the conduction of water from root hair region to the xylem vessels and consequently is responsible for continuous absorption.

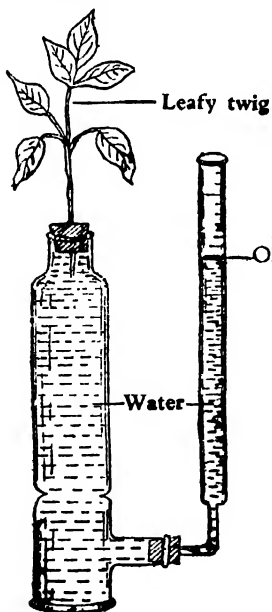


Fig. 4.3 An apparatus to find out the rate of water absorption in plants.

(ii) *Osmotic pressure of root hairs*—It helps in the absorption of water ; the rate of which increases with gradual increase in the osmotic pressure of the cell sap of root hairs.

(iii) *Guttation, transpiration etc.*—An increase in the rate of absorption of water takes place by the removal of excess of water by guttation, transpiration etc.

(iv) *Root anatomy*—Anatomy of the root in some cases is responsible for the absorption of water by land plants. Thus the characteristic absence of thick walled cells in the cortex and in the endodermis makes the movement of water easy.

4.7 Experiments on water absorption :

(i) *To show the phenomenon of water absorption*—Insert a *Peperomia* plant (with its complete root system) through a cork in a conical flask containing 1–2% solution of eosin. Now, the whole set is kept for sometime. After about an hour narrow streaks of red coloured solution are observed in the transparent stem of the plant indicating clearly that the red coloured solution has been absorbed by the root system and translocated upwards through stems and leaves.

(ii) *Rate of water absorption.*—Take a wide mouthed bottle (calcium chloride tower may be used) with a graduated side tube fixed with the bottle at its lower

end through a cork. Now, fill the whole apparatus with water and insert a small rooted plant through a cut cork with its root dipped under water. Make all connections air tight with sealing material and pour a few drops of oil on the free water surface of the graduated side tube. Mark the water level in the side tube (Fig. 4.3).

The whole set is now kept for a few hours. After that it will be observed that the level of the water in the side tube falls down considerably. Mark the final level at the end of the experiment from which the rate of water absorption can be calculated.

Let the initial level of the water in the graduated side tube = a ml

and the final level of the water after 2 hours in the side tube = b ml

∴ The amount of water absorbed in 2 hours = $(a - b)$ ml

∴ The rate of water absorption = $\frac{(a - b)}{2}$ ml/hour

4.8 Root pressure : As a result of water absorption, water is forced within the xylem vessels by the surrounding cortical cells with a force. This induces a hydrostatic pressure in the cortical cells of the roots and exerts its effect on the sap of the xylem vessels. This pressure is termed as **root pressure** i.e. the ability of a plant to force out liquid under pressure. Stocking (1956) defines root pressure "as a pressure developing in the tracheary elements of the xylem as a result of the metabolic activities of roots."

It is, therefore, a pressure exerted by the fully turgid cells of the roots and as a result of which water rises upto certain height within the xylem vessels. Thus, when a potted plant is decapitated a few cm above the soil surface, water is found to be forced out through the cut end. This is one of the most important manifestations of root pressure and is known as *bleeding*. Another manifestation of root pressure is the oozing out of water from the tips of certain herbaceous plants, this is known as *guttation* (for detail refer Chapter 6 article 6.7).

Root pressure and its related phenomena are important to majority of land plants which grow in moist, well aerated soil. It, however, shows a great daily as well as seasonal fluctuation, which attains its maximum value during day time (specially midday) and minimum at night ; root pressure has been found to be greater during spring than in other seasons.

It has been found by Stephen Hales that the magnitude of pressure varies in different plants and under various environmental factors. Under normal condition, root pressure value ranges from 1-1.5 atmosphere. Higher values upto 10 atm. (i.e. about 360 cm mercury) has been obtained in some cases. It has been observed that the root pressure generally decreases to an extremely low value when the transpiration is vigorous in the plant body. It, therefore, occurs when the absorption is sufficiently in excess of transpiration.

Root pressure is generally controlled by a number of external conditions. All the factors (i.e. soil temperature, soil aeration, concentration of solutes in the soil) which influence the absorption of water are indirectly related with the root pressure. Factors which

favour rapid transpiration in plants reduce the root pressure. Root pressure is also very much dependent on the respiratory enzymes of the plant body. Therefore, by blocking the supply of oxygen, the root pressure ceases. Since, all the factors are favourable for root pressure at night, the manifestation of this pressure can be best exhibited during early morning.

Mechanism of root pressure—As a result of continuous absorption of water by the roots, the cortical cells become fully turgid and are unable to absorb any more water. The concentration of root hair cell sap thus becomes lowered as compared to the surrounding cortical cells which are still in a higher concentration and as the two cells are separated by means of a semipermeable membrane, osmosis will take place between the cells and water from the lower concentration will move towards the higher concentration. As a result of this, the root hair cells again absorb water from the surrounding soil particles. In the mean time, the turgid cortical cell passes its water to another adjacent cortical cell and in this way cell to cell osmosis proceeds, resulting in alternate flaccidity and turgidity of the cells. This flaccidity and turgidity exert a pressure on the liquid content of the cell which ultimately forces the water into the xylem vessels (as the xylems are dead cells, no osmosis takes place between these and the living cells). The lateral movement of water according to Priestley (1920) is responsible for the development of a pressure known as *root pressure*.

Importance of root pressure—The phenomenon of root pressure is of vital importance to plant life. It shows the living nature of the cells, as no pressure exists when the root cells are killed by poisonous substances. As the process is directly related with osmosis it clearly suggests the semipermeable nature of the living cells.

It is the phenomenon by which upward movement of water through the xylem vessels takes place in a number of herbaceous plants.

Experiment to demonstrate root pressure—A healthy potted plant is cut a few centimeters above the soil surface. The cut tip is fastened tightly by means of a rubber tubing with a glass "T"-tube. Connect a manometer (whose narrow arm is graduated) with the side arm of the "T"-tube. Completely fill the T-tube with water. Now, close the upper end of the T-tube by means of a rubber cork and make all connections air tight by vaseline or sealing materials. The level of mercury in the narrow vertical tube of the manometer is noted

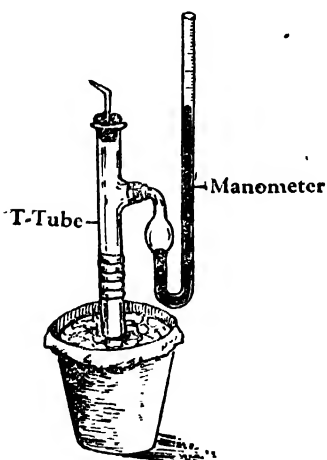


Fig. 4.4 Experiment demonstrating root pressure.

(Fig. 4.4). Now the pot is watered adequately and keep the pot as it is. After several hours the level of the mercury in the manometer is found to rise considera-

bly. Difference between these two readings gives the quantitative measurement of the root pressure exerted by the cut plant materials under that condition.

Initial level of mercury at the beginning of the experiment = a ml

Final level of mercury after the end of the experiment = b ml

Therefore, the increase in the mercury level due to root pressure = $(b - a)$ ml

4.9 Absorption of mineral salts : Besides water, plants normally take chemical elements from the soil in inorganic form. It is important to note that the plants absorb these elements not as molecules but as ions and mainly through the root system. When there is a net movement of solutes across the cell we call it *absorption* and when this absorption consequently increases the concentration of the cell sap inside than outside, we call it solute *accumulation*. In some cases, this movement is controlled by some physical forces such as diffusion and in that case free movement of the molecules or ions takes place. We can call this movement as *passive* or non-metabolic absorption. In other cases, however, the movement of the solutes occurs in opposite direction and at different rate. In such cases it is always involved with the utilization of cellular energy and is said to be *active*.

It was once supposed that the solutes mainly entered the plant cells along with the water molecules by the process of osmosis. But this statement is erroneous as it has been found by Hoagland in 1944 that the region of most active water absorption does not coincide with the region of rapid solute absorption. The factors which influence water absorption do not influence the absorption of mineral salts. Moreover, during active transpiration the absorption of water is found to be more rapid when the accumulation of solutes is found to be minimum. These clearly indicate that the solute particles can not be swept in with the water current within root cells.

It was also believed by many workers that the absorption of mineral salts takes place simply by diffusion process. Although a small fraction of the mineral salts is taken by diffusion, two other important mechanisms i.e. *salt accumulation mechanism* and *ionic exchange mechanism* are involved in the process.

SALT ACCUMULATION MECHANISM : The theory was first proposed by Hoagland and others in 1923 while working with *Nitella*. In this mechanism the salts are absorbed or accumulated in plant cells, concentration of which are greater than the external concentration of some salt in the surrounding medium. By this mechanism accumulation of both cations and anions takes place in equal quantities. Accumulation of greater amount of ions in the cell sap than the surrounding medium takes place due to diffusion of the ions *against a concentration gradient* i.e. from a region of lesser concentration to a region of greater concentration. This theory is also known as *active solute absorption*.

Careful studies have shown that the absorption of bromide, chloride and nitrate by green plants are influenced in the presence of light which was explained by Hoagland and Davis (1925-27 ; '33) as

due to increased metabolism and growth as a result of photosynthesis. Thus, there is an intimate relationship between salt absorption and energy relation of the cell. It has been shown by Steward and others (1935-36) that when aerobic metabolism is high with the liberation of more respiratory energy, potassium and bromide can enter the cells against the concentration gradient.

IONIC EXCHANGE MECHANISM : Theories put forward to explain the absorption of ions by plants usually involve the presence of a *carrier* in the cytoplasm which is able to combine with anions.

The general scheme of the operation of a carrier mechanism in ion uptake is shown in Fig. 4.5. The hypothetical salt KA is dissociated into cation (K^+) and anion (A^-) in the external solution. This anion (A^-) now combines with a carrier (C) on the cytoplasmic surface, the carrier-ion-complex then moves across the cytoplasm and near the vacuole in the inner side, the anion (A^-) is set free from the complex and accumulated in the vacuole whereas the carrier is again regenerated and activated to unite with a new anion. Cations and anions have separate carriers and when uptake of anions is taking place actively in carrier system, cations are moving passively along the electrical gradient developed due to accumulation of negatively charged anions at the inner surface.

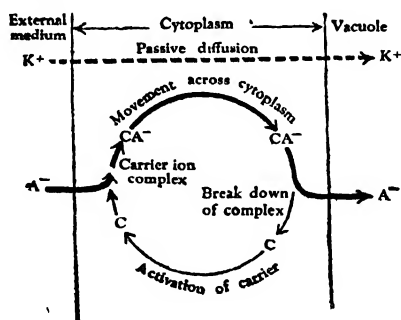


Fig. 4.5 General scheme for the operation of a carrier system in the uptake of ions.

This carrier contains iron porphyrin combined with protein (hemoproteins) and Lundegardh (1950, '54) suggested that this carrier system in cells is the cytochrome system which can exist in two forms :

- (a) Oxidised form Cyt^{+++} (ferric cytochrome)
- (b) Reduced form Cyt^{++} (ferrous cytochrome)

At the outer level, an anion (A^-) simply passes by diffusion through the cell membrane and is attracted by ferric cytochrome (Cyt^{+++}). As soon as the cytochrome-anion-complex ($Cyt^{+++}A^-$) comes in contact with an electron (e^-), the anion is released which again is caught by another cytochrome (Cyt^{+++}). In this way anions move from one cytochrome to another through this system. According

to Lundegardh there is a constant wave of electrons moving from inner surface to outer surface and owing to such movement of the electrons, anions move in opposite direction i.e., towards the inner surface. At the inner level anions are released from the cytochrome and given up to the vacuole of the cell.

According to this theory the main source of this electron (e^-) is the dehydrogenase reaction on the inner surface to produce protons (H^+) and electrons (e^-).



The H^+ liberated is then exchanged for the cations (K^+). This passes passively to balance the potential difference caused by the accumulation of anions on the inner surface.

The reduced carrier (Cyt^{++}) then loses an electron at the outer level and it becomes oxidised (Cyt^{+++}) which immediately travels

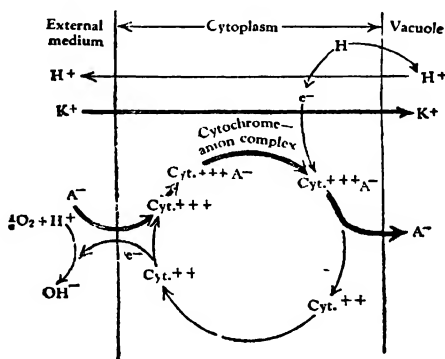
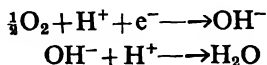


Fig. 4.6 Lundegardh's scheme for the absorption of ions in plant cells.

along the cytoplasm and thus repeating the process. The electron which is liberated at the outer level reacts with oxygen in the following way.



Since, this anion uptake involves utilization of metabolic energy, it is, therefore, not surprising that it is related to respiration. Decrease of respiration rate due to lack of oxygen or due to action of certain inhibitors, causes decrease in 'active' ion uptake. Thus Lundegardh claimed that the rate of oxygen uptake of the absorbing cells was due to (i) normal or 'ground respiration' unconnected with ion uptake and (ii) whose magnitude was determined by the rate of anion uptake. The latter type of respiration is termed as 'anion' or 'salt respiration'.

Thus, the amount of respiration increased over normal respiration by transferring a plant or tissue from water to a salt solution is known as **salt respiration**. Lundegardh's hypothesis suggested that four monovalent anions are absorbed per oxygen molecule in 'anion respiration' and that all anions stimulate respiration.

Although Lundegardh's hypothesis gives a clear picture of how the metabolic energy might participate in the absorption of ions, still it is not universally accepted and faced a number of severe criticisms. Thus, Robertson, Wilkins *et al* (1951) found that the chemicals which inhibit oxidative phosphorylation, increase respiration but decrease salt absorption. It shows that phosphorylation should be considered in explaining the mechanism of ion accumulation. The original idea of Lundegardh that only anions can stimulate respiration has been strongly criticised by Handley and Overstreet (1955),

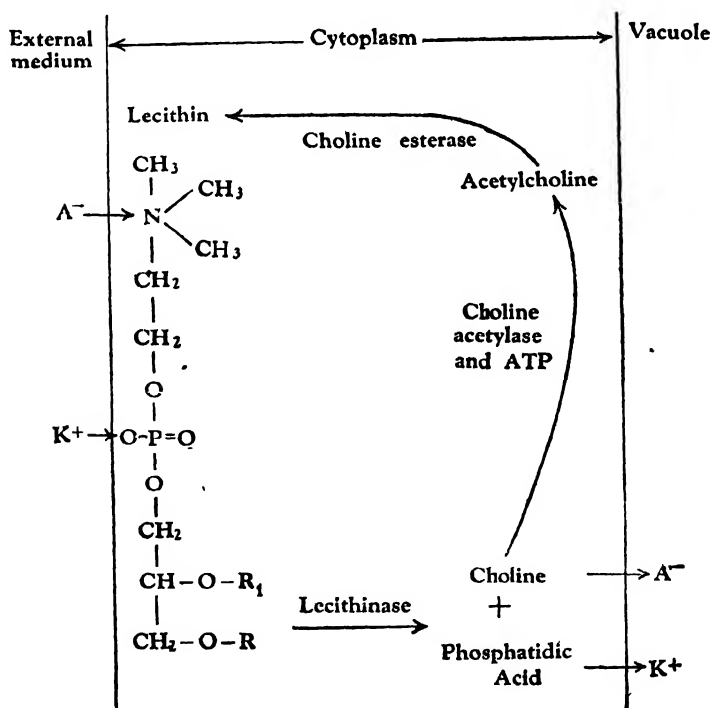


Fig. 4.7 Bennet-Clark's scheme for absorption of ions in plant cell. The diagram shows the cyclic formation of phospholipid, lecithin.

who showed that the absorption of both sodium (Na^+) and potassium (K^+) can stimulate respiration. Further, if one carrier is postulated for all anions, it fails to explain how there is no competition in uptake of different anions. Finally the respiratory cytochrome system is entirely confined to the mitochondria.

The idea of Lundegardh, although untenable, it stimulated research into the mechanism of salt accumulation. All the subsequent workers mainly concentrated their ideas in the chemical nature of the carrier. Thus in 1952, Goldacre suggested that there is an ordered contraction and unfolding of protein molecules oriented along the membrane of the vacuole. The contraction of protein molecule draws the ions through the membrane by utilizing ATP, the universal source of energy in the cellular metabolism. This act of contraction could lead to the liberation of the ions. Unfolding of the protein molecule would reset the trap for attaching new cations and anions. According to this theory, the carrier molecule is amphoteric (capable of binding cations and anions). Although this theory evades a major criticism of Lundegardh's hypothesis, still it is open to criticism.

In 1956 Bennet-Clark suggested that the carrier is a protein associated with the phospholipid, *lecithin*. Here also the carrier is amphoteric in nature. According to this hypothesis, the basic choline group is associated with binding anion (A^-) and the phosphatide is regarded as an active centre for binding cations (K^+). Liberation of the ions in the inner surface takes place by the decomposition of lecithin by the enzyme lecithinase. The regeneration of the carrier takes place through acetylcholine obtained by the activity of enzyme choline acetylase and ATP as a source of energy.

Although the experimental evidence in support of this theory is lacking, but it faces the difficulty in demonstrating the presence of the required number of phospholipids in the cell membrane to correspond with the known competitive groups of cations and anions.

4.10 Antagonism of salts or ions : In the preceding article, mainly the behaviour of cells to single ion or single salt has been discussed. But under physiological condition, cells and tissues are always in contact with media containing a variety of ions and the behaviour of the cell depends on the balance of the inorganic ions to which it is exposed.

The presence of single salt of calcium, sodium, magnesium etc. increases the permeability of the cell and causes injury to the cell. It has, however, been observed by Osterhout that the addition of second salt or in other words a mixture of various salts causes hindrance for the entry of the salts within the cell and consequently decreases the permeability of the cell membrane. *This phenomenon of the opposition of the salts or ions to enter the cells because of the presence of other salts or ions is known as antagonism.* Under certain conditions sodium chloride increases the permeability of the cell membrane. If, however, small amount of calcium chloride is introduced in the medium, the effect of permeability gradually diminishes.

It has been observed that when sea plants or animals are placed in a solution of sodium chloride having the same concentration as that of sea water, the plants or animals die very soon ; if small

amount of calcium, magnesium etc. are added then they do not die and live normally. From this, Ringer (1882) and Loeb (1889) concluded that the solutions of single salts are much more toxic in their action than the solutions of two or more salts. This toxic property of a single salt is destroyed when other salts like calcium, magnesium etc. are added. In sea water, several salts are present in solution which are able to antagonise the toxic effect of each other. Na^+ ions always decrease the entry of K^+ ions. Similarly for anions NO_3^- ions always retards the intake of anions such as SO_4^- .

It is obvious from above observation, that there exists a balance between the ions when they are in a solution outside plant cell, in order to maintain the low permeability for the living cell. Such a solution, where the toxic effect of the different individual ions is mutually neutralised, is called a balanced solution. Thus the sea water, fresh river water or water of the pools are suitably balanced for the cells in which they bathe.

SELECTED QUESTIONS

1. Describe different types of water present in soil.

Refer article 4.2

2. Show how the composition of soil affects the water relation in plants.

Refer article 4.1

3. What do you understand by available soil water? Explain unavailable water, gravitational water and hygroscopic water. What is the relative importance of these for the welfare of the plant?

Refer article 4.2 and 4.3

4. What do you understand by wilting coefficient?

Distinguish permanent and transient wilting. How can these two be determined?

Refer article 4.3 and for last part refer topic *permanent wilting percentage* in article 4.4

5. Explain the process of water absorption in land plants with reference to relative importance of the active and passive absorption theories in the process.

Refer article 4.5

6. How should a plant and its environment be treated so as to favour the most rapid absorption of water by roots?

Refer article 4.6

7. Describe the various external conditions which affect water absorption by the roots.

Refer article 4.6

8. Critically describe how water enters and leaves a plant body. Are these 'active' processes?

For the entry of water refer topic *active water absorption* in article 4.5 and for leaving of water refer *mechanism of transpiration* in Chapter 6 article 6.4.

9. Distinguish between a 'dry soil' and a 'physiologically dry soil'.

Refer topic *water content of the soil or available soil water* in article 4.6

10. Write notes on root pressure and its importance in plant life.

Refer article 4.8

11. Explain how plants absorb salts from the soil by roots.

Refer article 4.9

12. Give a critical account regarding the absorption of ions against a concentration gradient.

Refer article 4.9

13. Write notes on antagonism of ions and a balanced solution.

Refer article 4.10

14. How do you determine osmotic pressure in plants ? Discuss its importance in passive and active absorption of water by cells.

For first part refer Chapter 3, article 3.3

For the second part refer article 4.5

Majority of land plants obtain their necessary amount of water from the soil. Some quantities are lost during transpiration and some are utilized in other physiological processes. Hence water must move from the region of absorption through the intervening tissue to the tissues in which they are utilized or to other organs from which water passes out. This phenomenon of *the movement of water against the force of gravity is called conduction or translocation of water.*

The water which moves through the plant organ is not in a pure form, but it contains considerable amount of dissolved inorganic matters. The whole liquid content of water and minerals is known as *xylem sap*. So, whenever water moves through the plant it carries with it certain amount of solute matters. It is, therefore, better to define conduction of water as ascent of sap.

Entry of water mainly takes place through the epidermal cells and root hairs which after passing the cortex, endodermis etc. finally reaches the xylem vessels or tracheids of the root.

5.1 Path of water movement : It has been known for a long time that xylem or wood is the water conducting path in the land plants and the xylem consists mainly of dead lignified trachea or vessels and tracheids, which act as water pipes. Tracheids are elongated single cells which became thick walled in course of their development and then died. Vessels are formed from thick walled cells joined end to end. Soon, the partition wall dissolves and the cell content also disappears and thus they become hollow elongated tube like structures. Vessels are more efficient conducting system than tracheids. These conducting channels run from the roots through the stem and upto the veins of the leaves.

In small herbs, this conducting path is not considerable, whereas in large trees the path of water translocation may involve several hundreds of centimeters. From physiological and structural point of view, the course of water conduction in land plants consists of two parts. The xylem vessels comprise the important main part which is concerned in the dead cells of the xylem, the second part of water movement system consists of living cells through which water moves for only short distance. In the latter case, the small layers of root tissue from root hairs to cortical parenchyma are concerned ; the movement being due to suction tension by cell to cell osmosis.

That the wood vessels are the path through which water moves can
 * be shown by clogging the vessels of an *Impatiens* (Balsam) twig by

dipping it in molten gelatin jelly and then putting it in water, the plant is found wilting. Secondly, by ringing the cortex of the woody plant, it is proved that plants do not wilt so long as the vessels are kept intact. This proves definitely that the xylem vessels are the path of ascent of water and dissolved mineral substances (For detail see experiments in article 5.3).

5.2 Theories of ascent of sap : The mechanism by which water moves to the top of a lofty tree is a puzzle to the physiologists and which is still not satisfactorily solved. Hales (1769) was the first person to realize that there was a relationship between the transpiration of a plant and the upward movement of sap in the wood. Later workers observed that when the intact stem of a transpiring plant was cut beneath the surface of a dye solution, the dye rushed in, going both up and down the stem in the xylem. The upward movement of indicator substances such as spectroscopically detectable salts, dyes and radioactive isotopes can usually be related to the rate of transpiration. Several theories have been put forward by different scientists to explain the phenomenon of ascent of sap. All these theories fall within three categories : (i) vital theories, (ii) root pressure theory and (iii) physical force theories.

(i) **VITAL THEORIES :** Adherents of these theories believe that vessels through which translocation takes place are non-living and are in contact with living cells. For this reason, proponents of these theories suggest that upward translocation of water and other substances takes place by the vital activities of the living cells.

The main advocates of these theories are Godlewski (1884) and J.C. Bose (1923). Godlewski proposed that the movements of sap through the xylem are due to periodic changes in the osmotic pressure of the cells of the wood parenchyma and medullary ray cells. Due to increase and decrease in the osmotic pressure in these cells, water is driven out and is pumped into the vessels. His idea has been known as *relay-pump theory*.

Later, in 1923, Sir J. C. Bose proposed the *pulsatory movement theory* to explain the movement of water in plants. Bose's idea is really an elaboration of Godlewski's proposal of water movement. According to this theory, ascent of sap is due to the pulsatory movements of the endodermis. These cells continuously contract and expand due to pulsatory movements of these cells. When the cells contract the sap is pumped up to the next higher cell which consequently expands. This expanded cell in turn contracts again, thus pushing or pumping up the sap in the next higher cell. Thus the sap moves from one cell to another and so on.

The work of Strasburger (1893), however, shows that the upward movement of water is quite independent of the living cells of the stem as the sap continues to flow even when all the living tissues have been killed by picric acid. Later on, it has been observed by other workers that the leaves of the treated plant whose living tissues have

been killed previously, gradually wilt and wither. The main cause of this gradual wilt is that the killing of the stem causes the formation of substances which gradually plug the mouth of the xylem vessels. Further, the death of the cells causes the secretion of certain poisonous substances, which, when translocated to the leaves, cause their wilt. Although this theory apparently does not support the basic principle of the vital theories but the explanation of Strasburger's experiment indirectly supports that living cells of the stem have got an effect on the ascent of sap.

(ii) **ROOT PRESSURE THEORY** : It has been found that exudation of sap takes place from the freshly cut trunk or stem. This exudation is due to the pressure in the xylem sap as a result of root pressure. Root pressure may thus be referred to as an active process as the living roots are essential for it to occur. The idea of the movement of water in woody plants is based on this phenomenon. Although root pressure helps in some plants for the conduction of water to a little distance, still this phenomenon is not considered to be the principal mechanism for the movement of water, because this phenomenon of root pressure is not observed in most conifers and other gymnosperms which are among the tallest of trees. Secondly, the pressure which is set up is not sufficient to conduct water to the top of large trees. Values higher than 6 atmosphere have been found to be necessary for upward conduction of water, whereas root pressure more than 2 atmospheres is seldom obtained. Again in summer, while rapid transpiration is going on, exudation of sap even stops. Finally, the xylem sap under normal condition is in a state of tension instead of pressure, suggesting that root pressure is not an important factor in water translocation. A good example of this is guttation, a phenomenon caused by root pressure but noticeable only under low transpiration condition. For these reasons root pressure can not be held responsible for the rise of sap in large trees.

(iii) **PHYSICAL FORCE THEORIES** : These theories clearly suggest that physical phenomena and not the living nature of the cell are wholly responsible for the ascent of sap in plants. The following are the physical theories which are responsible for the ascent of sap.

(a) *Capillary force*—According to some physiologists, xylem vessels and tracheids occur in the plant in the form of small capillaries. These capillaries exert some force which helps to raise the water upto certain height of the stem. The main objection to this theory is that this force can raise the water in the stem only upto certain height. Further, the narrower the bore of the tube greater will be rise in the water column. It means that the tallest tree should have the vessels of narrowest bore, which does not tally with the anatomical organization of the stem. This theory cannot further explain the phenomenon occurring in the tall gymnospermous plants which have no true xylem vessels.

(b) *Atmospheric pressure*—According to some, water together with mineral salts is found to be moving upwards due to atmospheric

pressure. But this, however, can not explain the movement of sap in tall trees reaching 60 meters or more in height, as water can move upto a maximum height of only 9 meters due to atmospheric pressure. Further, the operation of atmospheric pressure requires a free exposed surface which does not exist in the xylem vessels.

(c) *The Cohesion-tension theory*—During transpiration water is lost from the leaves by evaporation through the micro-capillaries of the walls of the leaf parenchyma cells. This loss of moisture leads to the movement of water from the protoplasm and vacuole to the cell wall. This movement results in an increase in the osmotic concentration of the leaf parenchyma cells, which will in turn osmotically attract water from adjoining cells of lower osmotic pressure. In this manner an osmotic gradient is built up across the leaf to the contents of the xylem elements of the leaf. The deficit of water in the terminal cell in this gradient will be satisfied by the withdrawal of water from the xylem elements.

Molecules of water, although in motion, are also strongly attracted to each other. This cohesive force, together with the attraction which exists between the water molecules and the molecules of the wall of the tube (adhesive force), prevent the water columns from breaking when they are subjected to a pull. Thus, as a consequence of the pull resulting from the loss of water from the leaves during transpiration, the water in the xylem ducts is drawn up the stem under a tension or negative pressure.

This view of ascent of sap was first postulated by Dixon and Joly in 1894.

In its basic essentials, the cohesion tension theory relies on a purely physical mechanism. Probably the only living cells which are directly involved are the cells of the transpiring leaf. Kurtzman (1966) has recently shown that injection of trees with metabolic inhibitors and poisonous substances like picric acid and mercuric salts fail to cause any significant change in the speed at which the sap flows.

Cohesion hypothesis has been criticized on the grounds that xylem vessels are filled not with continuous columns of water under tension but with air and water vapour under reduced pressure (Preston, 1952). Further it has been demonstrated in the root pressure theory that water can exude from the cut stem without any leafy shoot and it completely devaluates this theory, as there is no transpiration occurring here. In spite of several weaknesses this theory still remains the most reasonable single explanation for the rise of liquids in plant body.

Considering all these foregoing theories regarding the ascent of sap in plants, it is evident, that not a single theory can explain fully the mechanism of water translocation. But an amalgamated effect of all these theories will be helpful in elucidating the process of water translocation in plant. The root pressure gives a pressure from below and active transpiration pulls the water column through the xylem

vessels which are in a cohesion tension, thus favouring the easy flow of liquids through the stem to the top of a lofty tree.

5.3 Experiments on conduction of water :

(i) *Palladin's method to show conduction of water*—Both the ascent of liquids through the stem and the effect of transpiration on the rise of liquids can be studied in this experiment.

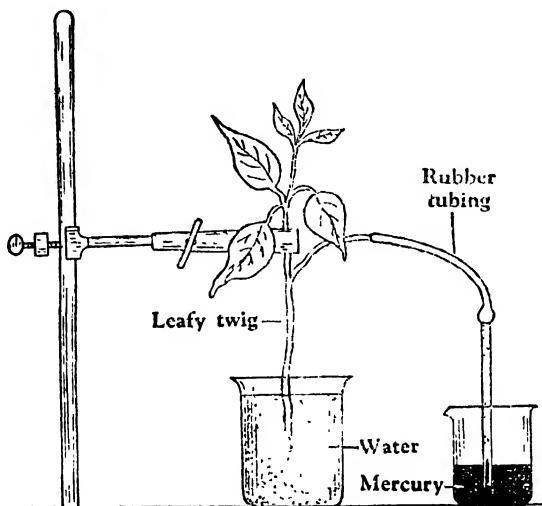


Fig. 5.1 Demonstrating the movement of water in a woody twig.

Take a leafy shoot and keep it under water. Remove all leaves from one of the side branches and cut it partly with a knife and attach a short piece of rubber tubing. Connect the other side of this tubing with a narrow glass tube (about 0.4 mm internal diameter). Then fill the glass tube with water and immerse it in a beaker containing mercury or boiling water containing a dye so that it can be easily seen (boiling removes all dissolved air that could form bubbles and exert a negative pressure on the water content). Make all connections air tight (Fig. 5.1). Now the water is continuous throughout the whole system extending from the mesophyll cells in the leaf, down through the xylem vessels of the stem into the rubber tubing and glass tube ending in the beaker at the base. After a few hours mercury or water will be found to rise in the narrow glass tube (exhibited by their colour if the water is coloured).

Under these conditions as water molecules are lost by transpiration from the upper surface of a leaf, the attraction of water molecules (cohesion) exerted as a pull causing mercury or coloured water to move up into the stem.

(ii) *Experiment to show the path of water conduction*—(a) Immerse a *Peperomia* plant in a breaker containing 2% solution of eosin. Keep it for some time and it should be observed that red colour appears to be coming up through the stem which indicates that the red colour after being absorbed by roots has ascended to the stem.

Now, cut transverse section of the stem and observe under a microscope. The red colour appears to be present only in the xylem vessels which shows distinctly that ascent of sap takes place through the xylem vessels.

(b) *Ringing experiment*—Take a potted plant and remove all the peripheral tissues (upto phloem and cambium) of the stem in the form of a ring leaving only the xylem intact. Keep the plant as it is after removing the tissues for 2-3 days. It should be observed that no wilting of the plant body takes place during the period which proves that the movement of water and liquids takes place through the xylem vessels and not through the outer peripheral tissues of the stem.

(c) Take a leafy twig of *Vinca* and immerse the cut end in a strong solution of CuSO_4 for a considerable period. As a result of this treatment all the living cells of the treated region have been killed. If now such a twig is placed in a beaker containing coloured water, no wilting of the leaves will take place normally and since all the living cells have been dead it proves definitely that the living cells have got nothing to do with the movement of water in plants.

SELECTED QUESTIONS

1. What do you understand by 'ascent of sap'? How does the sap rises in the system and what is its path? How would you demonstrate experimentally the ascent of sap in plants.

Refer introduction of Chapter 5 and articles 5.1 and 5.2. For the last part of the question refer article 5.3

2. Discuss critically the various theories that have been put forwarded to explain the mechanism of ascent of sap.

Refer article 5.2

3. Trace the path of a molecule of water from the time it enters the root hairs until it escapes as water vapour from the leaf.

Refer article 5.1 and the topic *experiment to show the path of water conduction* in article 5.3

4. How would you demonstrate the following phenomenon in plant life: 'Transpiration acting as a suction pump'.

Refer article 5.2(iii)(c)

5. Why is not atmospheric pressure considered to be a factor in the upward movement of water through plants?

Refer topic *atmospheric pressure* in article 5.2

6. How water ascends tall trees?

Refer article 5.2

7. Briefly discuss the present knowledge of how the ascent of sap takes place in tall plants including a reference to the work of J. C. Bose.

Refer article 5.2 stress on the *vital theories*.

6.1 Definition of transpiration : Transpiration may be defined as the phenomenon of the loss of water in the form of vapour from the internal tissues of aerial parts of plants under the influence of sunlight and regulated to some extent by the protoplasm.

Transpiration is very common in all land plants. This release of water vapour and consequent loss of water takes place mainly through the stomata of leaves. Transpiration is not simple evaporation from the leaf surface but a phenomenon influenced and regulated by the living cells according to the physiological necessity.

6.2 Transpiration and evaporation : Evaporation is essentially a physical process in which water changes from a liquid to a gaseous form. Transpiration, on the other hand, is a vital physiological process.

Evaporation is a slow loss of water molecules to the unsaturated atmosphere from the free exposed surface among living and non-living bodies. Transpiration is restricted to living bodies only.

Evaporation is simply a loss of water molecules which do not involve any pressure whereas several pressures¹ which usually act on guard cells are required in the process of transpiration.

Although there is little difference between transpiration and evaporation, still transpiration is not a case of simple evaporation as the amount of water evaporated from any surface and the amount of water transpired from an equal area of living plant surface in a given time under similar atmospheric condition is not the same; the amount of water evaporated from an exposed area is always greater than the amount of water transpired from the living plant surface. Hence, it is generally held that transpiration is a modified process of evaporation regulated by the protoplasm.

6.3 Types and sites of transpiration : The water which is absorbed in excess is not all utilized by plants but on the other hand is expelled in the vapourised form from the leaves and other parts of plants. Major portion (80-90%) of water vapour diffuse out through the openings of the stomata—this is known as *stomatal transpiration*; some amount (10-20%) of water vapour is also lost from the epidermal cells through the cuticle of the leaves directly—this is known as *cuticular transpiration*. Sometimes, loss of water also takes place through the lenticels of stems and fruits and this is called *lenticular transpiration*.

¹ The evaporating water molecules may exert a pressure against walls of the container and the surface of the water which is known as *vapour pressure*.

The magnitude of water loss through the cuticular and lenticular transpiration is very insignificant as compared with the loss through stomatal transpiration. Under dry condition, however, when stomata are closed, the loss through cuticle and lenticel is important.

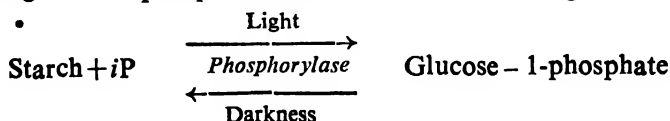
The most important organ of transpiration is the stomata which remain open during day time but close at night. As the gaseous exchange between the intercellular spaces of mesophylls of leaves and atmosphere takes place mainly through stomata, the diffusive capacity of stomata is an important factor. The amount of water transpired from the leaves is closely related to the diffusive capacity of stomata. During daytime owing to the increase in turgidity of guard cells, stomata are open and the rate of transpiration of water is consequently increased.

6.4 Mechanism of transpiration : The most interesting feature in the process of transpiration is that the stomata are the main pathway through which the gaseous exchange between a leaf and its environment takes place when they remain open during daytime and the gaseous exchange is retarded when the stomata are closed during night. The mechanism of transpiration is, therefore, broadly speaking the mechanism of opening and closing of stomata.

Stomata are the minute openings abundantly distributed mostly on the epidermis of the leaves. Each stoma consists of an opening between two highly specialised epidermal cells known as *guard cells*. The whole structure of guard cells and the opening constitutes stoma proper. The guard cells are semilunar or crescent shaped cells and are attached to each other by the curved ends of their concave sides and leaving a slit like opening.

The opening and closing of the stomata is mainly regulated by the changes in the turgor of the guard cells. Generally an increase in the turgor of the guard cells results in the widening of the stomatal aperture. The opening, however, is gradually narrowed when the turgidity of the guard cells decreases. This effect of the turgidity on the guard cells is due to the difference in the structure of the inner and outer walls of the guard cells. The cell wall of the guard cells towards the stomatal pore is thicker than the wall lying towards the epidermal wall. Therefore, as a result of increase of turgor, the outer walls are stretched more than the thicker side of the guard cell wall, resulting in the widening of the stomatal pore (Fig. 6.1).

Although there are several theories regarding the exact mechanism of opening and closing of stomata, the general concept is based on osmotic principle, according to which hydrolysis of starch (which is present in the guard cells) takes place in the presence of sunlight and as a result starch is converted into soluble sugar. The soluble sugar appears to be glucose-1-phosphate which is formed according to :



This reaction is catalysed by the enzyme *phosphorylase*, widely present in the chloroplasts of the guard cells (Yin and Tung, 1948). This conversion of starch to glucose increases the osmotic concentration of the guard cells which bring about the extension of the outer convex walls of the guard cells without any changes in the inner walls. Owing to such extension of the outer walls, the pore opens. In darkness, the process is reversed leading to the closing of the stomatal aperture.

Regarding the accumulation of starch in the guard cells it can be said that most of the starch in the guard cells is derived from the mesophyll cells. It has been observed by Lloyd (1908), Loftfield (1921) and Sayre (1926) that guard cells contain more starch in the dark than in light. The reverse effect has been observed in other epidermal cells and the mesophyll cells.

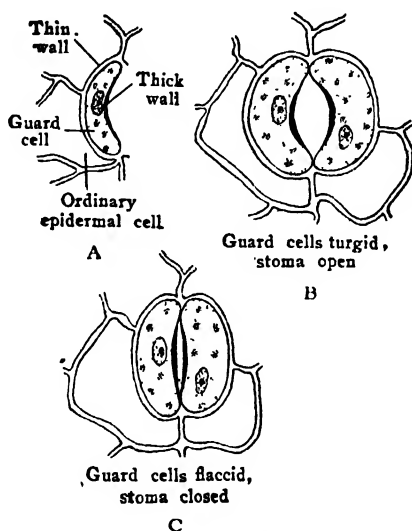


Fig. 6.1 Stomatal opening and closure.

A—a part of guard cell showing thicker wall abuts on the stomatal pore.

B—guard cells become turgid consequently thin peripheral wall bulge outward pulling the thick inner wall. This opens the stomatal pore.

C—when the guard cells become flaccid, the wall contracts and thus closes the stomatal pore.

Sayre (1926) and others have observed that opening and closing of stomata is very much sensitive to changes in pH.

It has further been shown that the conversion of starch to sugar is effected best at a higher pH value (nearly 7) than at lower value (pH5). According to Scarth and Shaw (1941) the equilibrium condition in the acidity and alkalinity of the cell content takes place in the following way. When photosynthesis stops at night, accumulation

of carbon dioxide results within the leaves, consequently acidity of the guard cell sap increases (decreasing the pH value). So in the dark, decrease in the pH favours the reverse reaction, accumulating starch within the guard cells. In presence of light, on the other hand, when all the carbon dioxide is utilized in photosynthesis the acidity decreases (increasing pH value).

At the higher pH ($pH7$) and in the presence of enzyme and inorganic phosphate starch is converted to glucose-1-phosphate. At the lower pH ($pH5$) the synthesis of starch takes place from glucose-1-phosphate. Since starch is osmotically inactive and glucose is osmotically active, the above reaction offers the possible explanation of the effect of pH on the movement of stomata.

In 1964, Steward, however, showed that unless glucose-1-phosphate is converted to glucose and inorganic phosphate, no appreciable change in osmotic relation can occur.

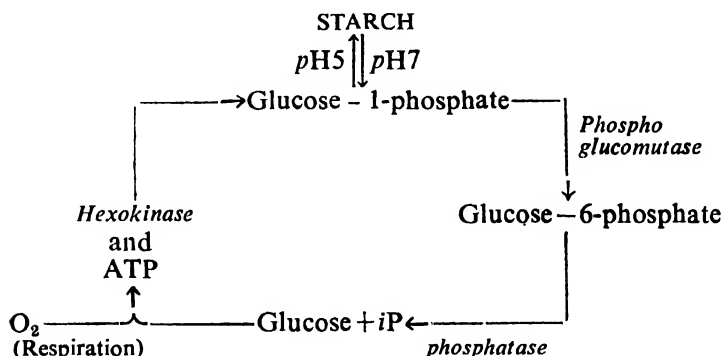


Fig. 6.2 Metabolic reaction as proposed by Steward (1964) in the opening and closing of stomata.

Steward (1964) showed that metabolic energy like ATP is necessary for the closure of the stomata. The ATP will undoubtedly be formed from respiration, this therefore necessitates the presence of oxygen. So, for stomatal closure, oxygen and energy is required whereas for opening they are not required.

Temperature also plays an important role in opening and closing of stomata. Under suitable environmental condition with the rise in temperature upto 30°C opening of stomata increases.

Water content of the mesophyll cells of the leaf is another factor which regulates the opening and closing of stomata. Low water content results in the reduction of turgor pressure of the guard cells consequently partial or complete closure of stomata results.

The stomata are very important organs from the physiological point of view. The opening and closing of stomata regulate the

gaseous exchange between the interior tissues of the leaves and outer surrounding atmosphere. The exchange is necessary for photosynthesis and respiration. Escape of water vapour during transpiration also takes place through stomatal openings.

6.5 Factors affecting transpiration : The rate of transpiration of a plant is greatly influenced by factors some of which are external and some are internal. Of the former the following are important : (i) light, (ii) atmospheric humidity, (iii) temperature, (iv) wind velocity, (v) atmospheric pressure and (vi) soil condition. Among the internal factors the following are important : (i) number of stomata and stomatal aperture and (ii) other structural peculiarities of the cell.

EXTERNAL FACTORS :

(i) *Light*—The rate of transpiration greatly increases in light and decreases in darkness. It has twofold effects on plant. Firstly, light causes stomata to open. As a result of wide opening of stomata the saturated interior cells of the leaf are exposed to or brought in contact with the outer atmosphere. Consequently, the rate of transpiration is increased in bright sunlight. Secondly, it increases the temperature of the leaf and thus affects the rate of transpiration.

Thus, the combined effect of light in causing opening of stomata together with increasing the rate of vapourisation of water, makes light the most important external factor affecting transpiration.

(ii) *Humidity*—It is also one of the important factors which influence loss of water by transpiration. As one of the most important phases of transpiration is the diffusion of water molecule from the intercellular spaces of the mesophyll cells of the leaves to the outer atmosphere it will, therefore, follow the simple law of diffusion i.e. the rate of transpiration increases or decreases with the changes in the relative humidity of atmosphere. When the moisture content in the atmosphere is less, transpiration is more rapid. When, however, the atmosphere is saturated with moisture the rate of transpiration is less.

The rate of transpiration, therefore, is more during the sunny summer days than cloudy rainy days.

(iii) *Temperature*—The rate of transpiration is dependent on the difference between the vapour pressure of the atmosphere and the intercellular spaces of the leaf which is termed as *vapour-pressure gradient* and this vapour-pressure gradient is greater with the rise of temperature. So, when there is a greater vapour-pressure gradient the higher is the rate of transpiration.

With rise of temperature upto certain limit, therefore, there is an increase in the rate of transpiration.

Temperature has got an influence on the diffusion of the water molecule through the stomata. Greater the temperature, the more rapid is the rate of diffusion and hence it indirectly helps in the transpiration process, since the stomata generally close at temperature $\pm 0^{\circ}\text{C}$ whereas an increase of aperture with increase of temperature upto about 30°C .

(iv) *Carbon dioxide concentration*—It has been observed that plants put in CO_2 -free air the stomata remain open even in the dark. Conversely, the stomata close in an increase CO_2 concentration even in light. CO_2 concentration in the intercellular space of the leaf in the vicinity of a stoma is of great significance than the CO_2 concentration in the air or elsewhere in the leaf. Thus if the stomata are transferred from high CO_2 concentration to a CO_2 -free air in the dark they do not reopen readily mainly because the CO_2 level in the intercellular spaces still remains high. If, however, the plant is illuminated, reopening takes place rapidly, because the level of CO_2 concentration is reduced by photosynthesis. In the variegated leaves the stomata in the non-chlorophyllous regions behave in the same way as those in the green regions, but do so very slowly. This is due to delay in the lowering of CO_2 level in the intercellular spaces in the non-chlorophyllous region of the leaf.

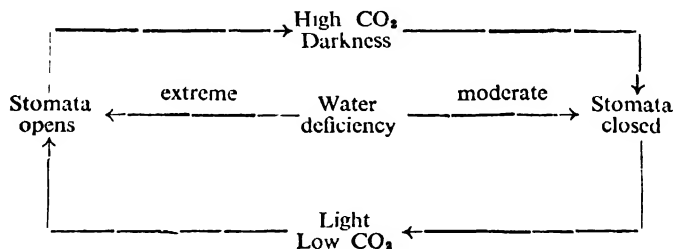


Fig. 6.3 Relation of stomatal opening to light, CO_2 concentration and water deficiency.

(v) *Wind velocity*—Increase in the wind velocity usually increases the rate of transpiration by removing the water molecules from the neighbourhood of the leaf. In the quiet atmosphere there is a tendency of the water vapour to accumulate in the vicinity of the transpiring leaves. This causes a decrease in the vapour-pressure gradient and consequently decrease the rate of transpiration. When, however, wind is blowing with sufficient velocity, the saturated atmosphere surrounding the transpiring leaf surface is being continuously renewed by new air currents, bringing drier air into direct contact with the leaves. This increases the gradient of diffusion and consequently increases the rate of transpiration.

The rate of transpiration increases more when the gentle breeze prevails than at high wind velocity. At high wind velocity the rate decreases due to closure of stomata.

(vi) *Atmospheric pressure*—It has got a minor effect on the rate of transpiration by plants. But usually a fluctuation in the pressure causes an inverse change in the rate of transpiration. Thus, higher the pressure, the lower is the rate of transpiration. So, in higher altitude where the atmospheric pressure is low, the rate of transpiration is high.

(vii) *Soil conditions*—The nature of the soil indirectly affects the transpiration as the soil condition is concerned mainly with the absorption of water by plants. At a high concentration of soil solutes, there will be less absorption of water by plants as a result of which there will be a decrease in the rate of transpiration. All the factors which directly affect the rate of water absorption will indirectly influence the rate of transpiration by plants.

INTERNAL FACTORS: (*Structural features of the plant which influence the rate of transpiration*) :

Besides external factors, there are certain internal factors which influence the rate of transpiration greatly. The most important of these is the root-shoot ratio. The efficiency of absorbing surface (root system) and transpiring surface (leaf surface) control the rate of transpiration. Thus, if water absorption lags behind transpiration, a water deficit will occur which in turn will reduce transpiration. Parker (1949) observed an increase of transpiration rate with increase of root-shoot ratio. Beside this internal factor are size, arrangement and position of leaves and the number of stomata in leaves etc. The general structure of the leaf particularly the epidermis has influence on the rate of transpiration. The epidermis with thick heavy cuticle, waxy layer, epidermal hairs, shining reflecting leaf surfaces reduce transpiration to a greater degree. The compactness of tissues and air spaces within it are also important internal factors affecting the rate of transpiration. The more loose is the arrangement of the mesophyll tissue, the more is the rate of transpiration. So, xerophytes have compact mesophylls where the transpiration is less. The water retention capacity of leaves is another internal factor for regulating transpiration.

6.6 Significance of transpiration : Although water is found to be essential in the normal plant life yet large amount of water is being lost by the plants during transpiration. The probable explanation of such a behaviour is that it must have some beneficial effect on the plants. But the continuous loss of water during dry condition (in dry soil also) has on the other hand a harmful effect ; although this harmful effect is outnumbered by its beneficial effect. That is why transpiration is said to be '*a necessary evil*'.

The importance of transpiration in the life of the plant can be summarised as :

(i) *Role in the movement of water*—It has been found that the movement of water through xylem vessels is considerably favoured by

the active transpiration from the leaves. Active transpiration in the leaves causes an increase in diffusion-pressure-deficit (DPD) in the mesophyll cells of the leaves and since the water stream forms a continuous column from roots to the top most part of the plants, it speeds up the rates at which water will move to a considerable height within the xylem vessels. So, under high transpiration, the rate of movement of water through xylem is more rapid than at low transpiration rate ; but still it cannot wholly explain the process of conduction of water in plants as the force alone is not sufficient to raise water to a considerable height.

(ii) *Role in the absorption and upward translocation of mineral salts*—It has been found that an accumulation of large amount of mineral salts takes place during high transpiration. The probable explanation is that the mineral salts are swept into the plant body with the absorbed water. But this explanation is erroneous as it has now been proved that the process of water uptake by the roots is quite different from mineral salt absorption and the two processes are quite independent of one another. Hence, the mineral salts cannot enter in the same process mixing with water. Although experimental works of Broyer and Hoagland (1943) suggested that under certain conditions the increased transpiration may result in an increased accumulation of mineral salts, but there is no consistent correlation between the transpiration and mineral salt accumulation.

After absorption, the mineral salts continuously move to the xylem vessels where they mix up with the water and move upwards together with water column. Since the upward movement of water is enhanced considerably by active transpiration, it has the same role in the upward movement of the mineral substances.

(iii) *Role in reducing the temperature of the leaf*—Another beneficial effect of transpiration is reducing the temperature of the leaves, which enables them to function normally even in the brightest sunlight without injury.

When the sunlight falls directly on the leaves, the radiant energy is absorbed which increase the temperature of the leaves and unless there is mechanism for dissipating a part of the leaf's temperature there is every possibility of the leaf temperature reaching beyond the lethal point. But leaf temperature seldom attains a higher level than the surrounding atmosphere, evidently there must be some energy-dissipating mechanism at work in the leaves which prevents the high temperature rise and transpiration is found to play an important role in this dissipation mechanism.

Of the total light falling on the leaf surface about 50% is absorbed by the leaf which is converted to heat energy and it can raise the temperature of the leaf to a point which is fatal to the protoplasm. Part of this temperature is then, however, dissipated by the process of transpiration. Transpiration is, therefore, found to play an

important role in maintaining leaf temperature in a balanced condition and prevent overheating of the leaves.

(iv) *Role in giving out excess water absorbed by the plants*—Plants have no mechanism to absorb exact amount of water required for their metabolism. They always absorb excess water from the soil under favourable condition and this excess water is given off by the plants during transpiration and which should have otherwise disbalanced the normal activities of the plants. This loss of water has also a cooling effect and this keeps the plant being overheated.

(v) *Role in maintaining optimum degree of turgor in cells*—According to Ivanov, for the flowering and fruiting of plants there must be certain saturation deficit within the cells and this optimum degree is maintained by transpiration of the plants.

In spite of all these above beneficial effects transpiration is often said to be very detrimental to the plants. Under condition of rapid transpiration (even when there is an adequate water supply) and under inadequate water supply in the soil, the proportion of water content in the cells decreases and the cells become less turgid. Thus during active transpiration a series of other activities including the decrease in the turgidity of the cells and decrease in the photosynthetic activities may be observed and the end result is a check in the growth of the plant. Under these conditions transpiration is said to be definitely harmful instead of being beneficial.

6.7 Other methods of water loss: Water is not always expelled from the plant in vapour form, but may also exude out from certain regions of the plants intermittently in liquid form. When *the escape of water takes place from the tips or margins of the leaves in the vicinity of the mid vein or veinlets from the uninjured leaves, it is called guttation*. In many cases the oozing of the liquid content may take place from the water conduction tissues when ruptured. This phenomenon of excretion is known as **bleeding**. Another type of excretion is the **secretion** which consists mainly of exudation of water and solutes from certain specialized cells, constituting a gland found in various parts of the plants.

All the processes of exudation are basically same and an account of them is given below.

(1) **GUTTATION**—This process is generally favoured when active water absorption takes place by roots, but there is a reduced rate of transpiration. Many plants of temperate regions like *Impatiens*, garden nasturtium, *Colocasia*, grasses, *Lycopersicum* etc. readily exhibit this phenomenon. In most temperate regions particularly during late spring the condition can be more favoured for the easy absorption

of large amount of water than the water loss by transpiration which causes the development of a root pressure and consequently guttation occurs. This process generally takes place at late night or at early morning hours and can easily be confused with dew drops. But they can be distinguished by the fact that guttation occurs only at the tips or margin of the leaf lamina at the points of the veins; the dew, however, collects over the whole surface of the leaf. Again, since the guttation contains a mixture of solutes (carbohydrates, nitrogenous compounds, organic acids, mineral salts etc.) so when evaporated, the guttation water leaves an impression of salts at the tips or margin of the leaves; dew drops, however, leave no such impression.

Physiology of guttation—This process of water exudation usually takes place through certain specialized structures known as *hydathodes* or water stomata (refer *Studies in Botany* vol-1).

These are minute pores whose walls are unspecialised and incapable of movement so that the pores always remain open. Behind the pore is an air cavity below which there is a thin layered mass of parenchymatous tissues known as *epithem*. The xylem tracheids are placed just behind the epithem suggesting the ends of the vascular bundle.

Due to active root pressure the liquid content of the xylem vessels comes out in a thrust, as a result, minute droplets pass generally through the intercellular spaces of the epithem and ultimately collect at the mouth of the pore and ooze out as minute droplets from the tip or margin of the leaves.

(2) BLEEDING—In many cases the phenomenon of bleeding can be observed from the injured plant parts as an exudation of liquid content from these regions. This type of exudation can be seen in a number of herbaceous plants. The main cause of such an exudation is the development of pressure in the xylem vessels or in the sieve tube of the phloem. The oozing out of the sugary juice from the mapple tree, toddy palms, palm tree provides the best examples of bleeding in plants.

(3) SECRETION—Secretion is usually performed by specialised cells called *glands* which secrete water and other dilute solutions. Besides water, they also secrete certain enzymes in digestive glands, nectar glands of nectaries in majority of flowers. Moreover, there are oil glands, resin glands etc.

Secreted substances in the majority of cases are the byproducts of metabolism and not due to any development of pressure.

Many secretions play an important role in the life of the

plant. Others are of no use and are therefore known as *waste products*.

6.8 Experiments of transpiration :

(i) *Experiment to demonstrate the phenomenon of transpiration*—Take a healthy small potted plant. Cover the soil including the pot with a rubber sheeting or plastic material so that the moisture from the soil or from the surface of the pot can not escape. Take a bell jar and cover the pot including the plant with it and keep it in bright sunlight (Fig. 6.4).

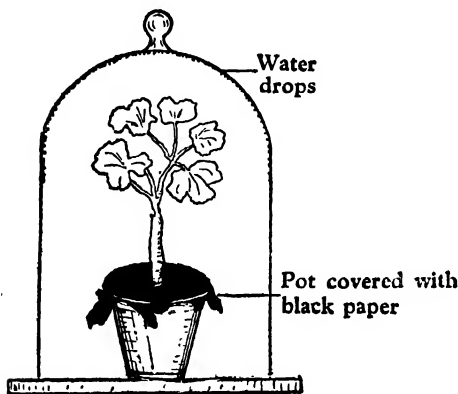


Fig 6.4 An apparatus to demonstrate transpiration.

As a control take another pot but without any plant. Cover it as usual and then the whole pot by means of another bell jar. After half an hour a film of moisture appears on the inner surface of the bell jar containing the plant. But no such moisture will be observed in the control set. In the first set due to transpiration water vapour will come out which in some cases be condensed as droplets of water on the inner surface of the bell jar.

(ii) *Experiment to measure the rate of transpiration*—The rate of transpiration¹ can be measured with the help of apparatus known as *potometers*. This is an indirect method of measuring transpiration of water absorbed rather than the actual amount of water loss during transpiration. This experiment is based on the assumption that the amount of water transpired is almost equal to the amount of water absorbed (although it is not the general rule).

A simple type of potometer was devised by Darwin and Acton (1925) (Fig. 6.5). It consists of a narrow tube with a broad end. The broad end is closed with a cork with a single hole. The whole tube is filled up with water and a leafy twig (cut under water) is inserted through the hole of the cork. It is then made air tight and placed in sunlight. As the transpiration proceeds, water is moved up in the narrow tube and its level gradually rises upwards. The narrow end is immediately dipped into a beaker containing water and the rate of movement of bubbles in the transpiration stream is counted by fixing a scale on the lower tube. Then the rate of transpiration can be calculated by $\pi r^2 \times l/\text{hour/sq cm}$.

πr^2 is the area of the bore of the lower tube and 'l' denotes the distance traversed by the bubble in the requisite time. The area of the leaves can be calculated by any one of the methods mentioned in experiment (vi).

¹The rate of transpiration means the amount of water transpired per unit area of the leaf surface. It is the intensity of transpiration and therefore can be expressed in g/hour/sq cm of the leaf surface.

In some cases the rates can be expressed in term of dry or green weight of the plant. The number of grams of water lost in accumulating one gram of dry substance is called **transpiration coefficient** or **transpiration ratio**. It differs in different plants and under different environmental condition.

Besides this potometer there are other types of potometers used now-a-days to determine the rate of transpiration. These are Ganong's and Farmer's potometers which have the same basic principle. Ganong's potometer consists of a narrow graduated horizontal tube which held two vertical wide mouthed tube—one of which fitted with a cork through which passes a leafy twig (cut under water) and the other acts as a reservoir and is fitted with a stop cock. The other end of the horizontal tube bends at right angle and at opposite side of the vertical wide mouthed tubes (Fig. 6.6).

The whole apparatus is filled with water and a leafy twig is inserted through the cork of the vertical tube. Keeping the stop cock closed make all connections air tight. Now allow the twig to transpire for a short period as a result water will be moved upwards in the lower bent tubes of the potometer. Now immerse the potometer in a beaker containing water (which may be coloured with eosin) as a result, a bubble will be formed which will move and fix in the horizontal tube. Now fix the apparatus with a clamp in this position. As the water will move due to transpiration the bubble will appear moving in the horizontal graduated tube. Note the time taken to move the bubble through a specific length. When the bubble moves to a considerable distance and comes near one end of the tube, then by opening the stop cock the bubble can be pushed back to its original position and the experiment can be repeated several times.

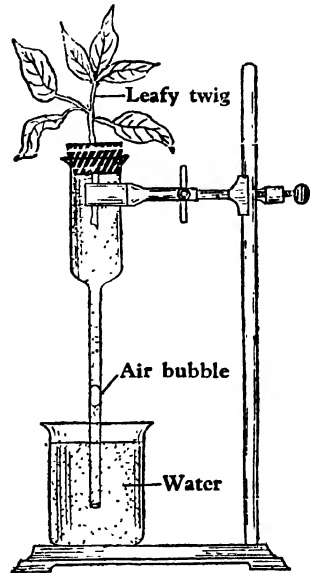


Fig. 6.5 True potometer—the rate of bubbles moving within the tube is measured.

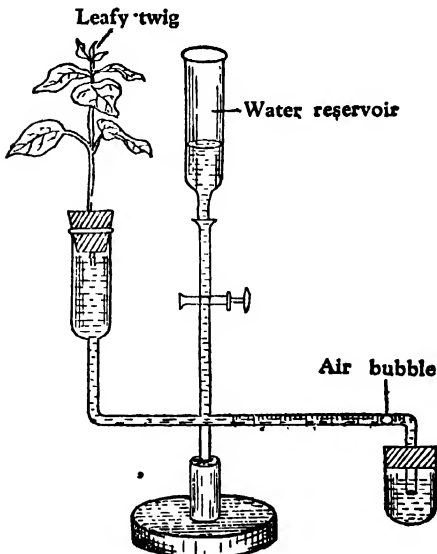


Fig. 6.6 Ganong's potometer.

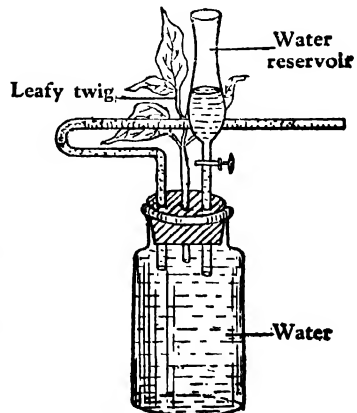


Fig. 6.7 Farmer's potometer.

The rate of transpiration can be obtained by the following calculation.

Position of bubble at the beginning of the experiment = a cm

Position of bubble after 30 minutes = b cm

Therefore, the distance traversed by the bubble in

$$30 \text{ minutes} = (b - a) \text{ cm} = 'l' \text{ cm}$$

Volume of water transpired in 30 minutes = $\pi r^2 \times l$ ml

∴ Volume of water transpired from the twig in an hour

$$= \frac{\pi r^2 \times l \times 60}{30} \text{ ml}$$

Farmer's potometer has the same working principle as Ganong's and is a modification of the latter (Fig. 6.7).

(iii) *Measurement of transpiration rate (Quantitative)—By Conical flask*—The rate of transpiration can be accurately measured by various methods and can be expressed per unit area per unit time.

Take a 250 ml conical flask, fill upto its neck with water and insert a *Gardenia* or any suitable leaf (cut under water in order to maintain continuity of water columns) with its petiole remain deep within the water. Now pour some oil (non volatile) on the surface of the water, so that no evaporation can take place from that open water surface (Fig. 6.8) Weigh the whole set and keep the flask in a suitable place for transpiration. After one hour weigh the set again. The difference between these two weights gives the amount of water loss from the leaf in an hour.

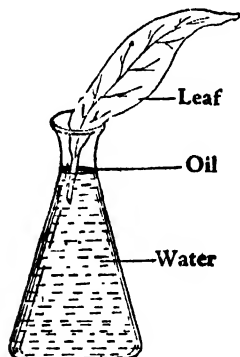


Fig. 6.8. A simple apparatus to find out the rate of transpiration.

Rate can be determined by measuring the area of the leaf [refer experiment (vi)] and can be expressed per unit area per unit time.

From this experiment correlation with the simple physical evaporation can be made [refer experiment (v)].

(iv) *Differential rate of transpiration from two surfaces of a leaf:*

(a) *Qualitative or hygrometric paper method*—Cello-tape is first cut into lengths (approximately 8.0 cm long). Tear these sections off the roll of the cello-tape and handle each piece by the middle of the cello-tape and the hygrometric paper will be placed. Stick the centre of the tape to a finger of the left hand and with the forceps in the right hand transfer a piece of cobalt chloride paper¹ to each side of the tape. The characteristic feature of the paper is that it remains blue when dry and turns pink when moistened.

Immediately fold the tape over a leaf of a potted plant (Fig. 6.9B) so that one piece remains on the upper leaf surface and the other on the lower. Care should be taken to seal tightly the tape completely covering the paper.

The length of time necessary for the paper to turn pink indicates the rate of transpiration from the two surfaces of a leaf.

(b) *Quantitative (by Garreau's potometer)*—The quantitative differential rate of transpiration from lower and upper surfaces of a leaf can be determined most effectively by this apparatus. It consists of two small wide mouthed jars which are placed face to face keeping a widely expanded leaf (the end of the twig is however

¹ Cobalt chloride paper was made by dipping strips of blotting or filter paper in 2% cobalt chloride solution and drying the same.

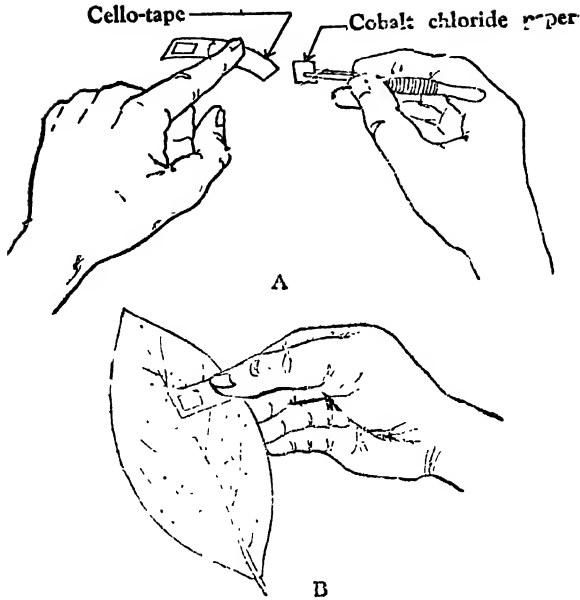


Fig. 6.9 Showing the arrangements for differential rate of transpiration with cobalt chloride paper.

kept in a beaker containing water) in between them. Before keeping the leaf in position some known amount of anhydrous CaCl_2 weighed and taken in two small tubes. Place one tube in upper and another tube on the lower glass jars with the corks, through which connect two manometers, to keep the vapour pressure within the jars constant. The rims of the jars in contact with the leaf surface are made air tight with vaseline (Fig. 6.10). The whole arrangement is now kept in a place favourable for transpiration and after one hour CaCl_2 tubes are taken out and weighed again. The increase in weight of the tubes indicates the amount of moisture absorbed by CaCl_2 . The difference between the initial and final weights of the tubes gives the amount of moisture liberated from the two surfaces of the leaf and thus indicates the

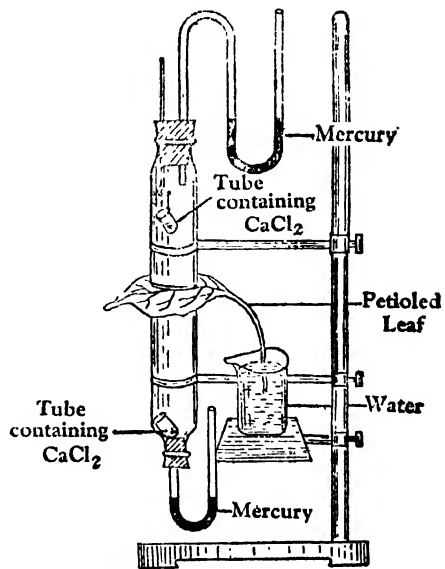


Fig. 6.10 Garreau's potometer for demonstrating differential rate of transpiration.

differential rate of transpiration from the same area of the upper and lower surfaces of a leaf.

(v) *Comparison of transpiration rate with the evaporation of water*—Determine the rate of transpiration through the given leaf surface from an unit area [refer experiment (iii) (a)].

Take a Petridish and half fill it with water. Now, weigh the Petridish and keep it in an exposed surface. After one hour weigh it again and find out the area of the evaporating surface by πr^2 . The difference between these two weights gives the amount of water evaporated from the particular area. Express the result in an unit area and compare it with the water transpired from the same unit area of the leaf.

(vi) *Methods of measuring leaf area :*

(a) *By graph paper*—Place the leaf on a mm graph paper and draw an outline of the leaf on the paper. The count the total number of large square blocks (1 large sq block \equiv 1 sq cm) and a fraction of it, if any, indicates the total area of of the leaf (Fig. 6.11).

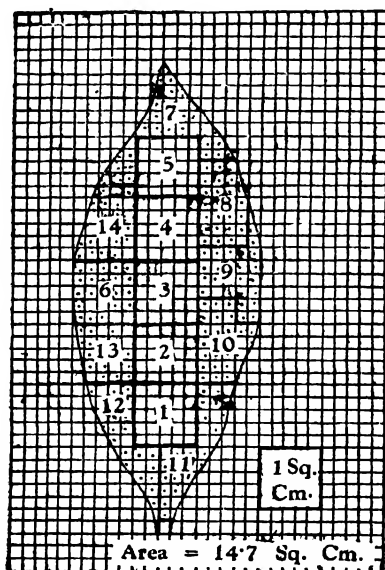


Fig. 6.11 To find out the area of a leaf by graph paper method.

(b) *By weighing*—Place a leaf on a card board and draw an outline of the leaf on it. Accurately cut out the leaf area and weigh the board (say 5 g). Now cut out known area (suppose 1 sq cm) from the board and weigh it. Suppose the weight of 1 sq cm block is 0.5 g

Therefore $0.5 \text{ g} \equiv 1 \text{ sq cm}$
 $5.0 \text{ g} \equiv 10 \text{ sq cm}$

\therefore the area of the leaf is 10 sq cm

(c) *By planimeter*—The main operation of the apparatus in determining the area of the leaf is to place the leaf on a board and keep the point of the instrument near one margin of the leaf and pass it around the margin of the leaf. The

result (area in sq cm) can be directly obtained from the scale and vernier attached on it.

(vii) *Determine the total number of stomata on a leaf*—With the help of a stage micrometer find the radius (r) of the field of vision of a given microscope which is exactly the half of the diameter of the circle. Then, find out the area of the field of vision of both low and high power by πr^2 . Now, peel off the lower epidermis of a leaf and count the number of stomata present under the field of vision of the microscope.

Find out the area of the whole leaf by any one of the above methods (refer experiment (vi)).

If the area of the field of vision = x sq cm

the number of stomata = a

and the area of leaf = y sq cm

then the total number of stomata of the leaf = $\frac{a}{x} \times y$

(viii) *Find out the stomatal frequency*—Stomatal frequency is generally determined by the number of stomata present per sq cm of the leaf. First, find out the area of the field of vision of the microscope [refer experiment (vii)] by means of a stage micrometer.

Peel off the lower epidermis of a leaf, mount it on a slide and count the number of stomata present under the field of vision. Take at least three readings from three different regions of the peeling and then take the average count.

If the area of the field of vision = x sq cm

Number of stomata in the above field = a

$\therefore x$ sq cm contains a number of stomata.

$\therefore 1$ sq cm contains $\frac{a}{x}$ number of stomata and which is equivalent to the stomatal frequency of the given leaf.

(ix) *To find out the stomatal opening :*

(a) *Lloyd's method*—Peel off the lower epidermis of a *Rhoeo discolor* leaf and plunge it immediately in a beaker of hot alcohol. The alcohol fixes the stomata so that no further movement of the stomata takes place. It is then mounted on a slide and examined under a microscope. The opening of the guard cells is then calculated by a standardised ocular together with the area of opening. Since the area of the opening is ellipsoidal in nature, it can be calculated by $\pi (a \times b)$, where a and b represent the halves of the two axes of the ellipse.

(b) *Impression method*¹—Take a leaf from a healthy potted plant and smear its lower surface with durofix and keep it for sometime. After half an hour the durofix will be dried up and now take out the film from the leaf. This film will carry the impression of the stomata of the leaf which on examination under the microscope gives the exact area of the stomatal opening [refer experiment ix(a)].

(x) *To find out the degree of stomatal opening by Darwin's porometer*—It consists of a 'T'-shaped glass tube, both the arms of which are fitted with rubber tubing. One side arm is fitted with a screw cock, the other arm, however, is connected to a cup. This cup is fixed on the lower surface of leaf, the margin of which is sealed with vaseline to make it air tight. The long vertical glass tube is kept in a beaker containing water. Now, the side arm tube is unscrewed and sucked, as a result of which water will move upwards in the vertical tube. The screw is now closed at this position, mark the level of water in the vertical tube and keep it for sometime. If the stomata remain open the level of the water will fall

¹ It can be done by using collodion (1 g of pyroxyline in 6 ml of alcohol and 20 ml of ether) smear on the leaf. When it hardens it can be stripped off and it will retain the impression of the surface.

down considerably and the rate of fall of the water provides a direct measure of the rate at which air passes out through the stomatal opening (Fig. 6.12).

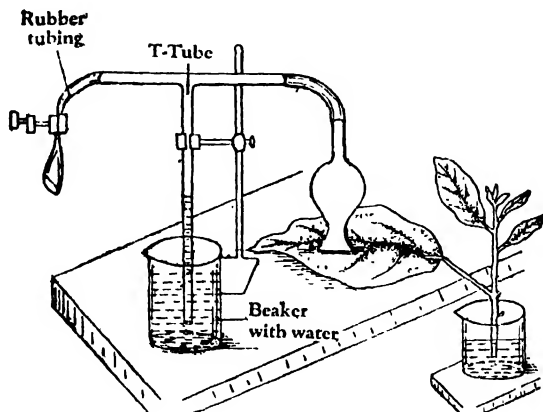


Fig. 6.12 Darwin's porometer to find out the degree of opening of stomata.

If the stomata, however, remain closed no air can pass through stomata and consequently it can not exert pressure on the water column of the vertical tube and so the level of the water remains stationary.

(xi) *Determine the amount of water absorbed and transpired by plants*—The apparatus consists of a wide mouthed bottle with a graduated side tube attached at its base through a cork. The mouth of bottle is fitted with a cork through which passes a small twig (cut under water). The bottle is filled up with water and all connections made air-tight. A drop of oil (non volatile) is placed at the open water surface of the side tube to check the loss of water by evaporation from that surface. The level of the water in the side tube is marked (Fig. 6.13). The whole set is weighed in a pan balance and kept in a proper place. After one hour the set is weighed again and the level of the water in the side tube is also noted. The difference in weight gives the amount of water transpired and the difference in the level of water in the side tube gives the amount of water absorbed.

This experiment can also be done by a simple measuring cylinder. Take a small measuring cylinder and fill it upto its mark with water. Insert a leafy twig and add some drops of oil on its surface. Weigh the whole set (w_1 g) and mark the water level on the cylinder. Allow the whole set to transpire and after one hour weigh the set with leaf again (w_2 g) and note the change of water level. The difference in weight ($w_1 - w_2$ g) is the amount of water transpired whereas the difference in the level of water before and after the experiment indicates the amount of water absorbed by the twig in an hour.

(xii) *Experiment to demonstrate the suction force due to transpiration*—Take a narrow bored glass tube and insert a leafy twig (cut under water) through one of its open ends. (The insertion can be properly made by a rubber tubing joining the glass tube and the twig). It is then made air tight by sealing materials. Water is now poured through the other end and the tube is completely filled. The whole set is now put in a beaker containing mercury and the mercury level in the glass tube is noted (Fig. 6.14). It is then clamped to a stand and kept an hour for transpiration. After one hour the mercury level is found to rise in the glass tube to a certain height.

The suction force due to transpiration can be easily calculated by the formula $\pi^a h$ p.g dynes/cm², where π^a is the area of the bore of the glass tube, h is the

increase in height of the mercury column in the glass tube ; ρ is the specific density of mercury (13.6) and g is the gravity (981 dynes).

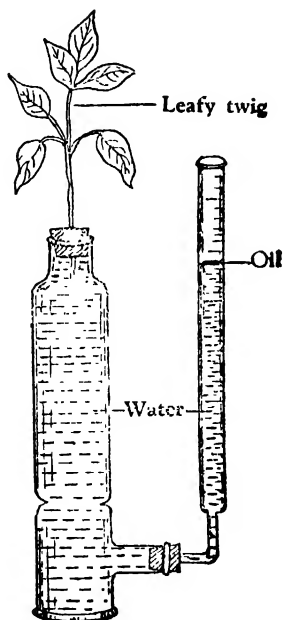


Fig. 6.13 An apparatus for simultaneous determination of amount of water absorbed and amount of water transpired.

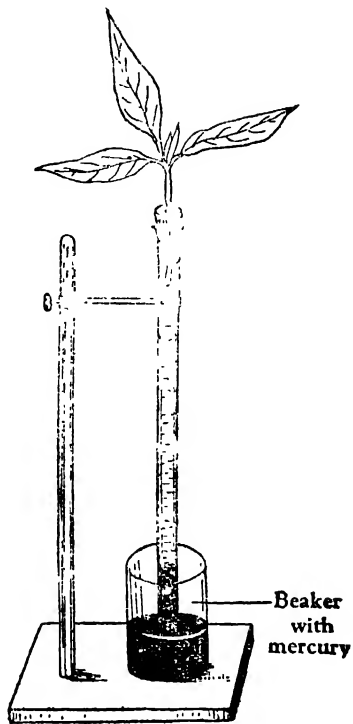


Fig. 6.14 An apparatus for demonstrating suction due to transpiration.

(xiii) *To determine the transpiration index*—Transpiration index is the ratio of the time in seconds taken to change the colour of cobalt chloride paper from a free evaporating surface (S) and a transpiring surface (E) and can be expressed as :

Transpiration index = $\frac{S}{E} \times 100$, it is convenient to multiply it by 100 in order to get the result in percentage basis.

Take two equal pieces (about 1 sq cm) of cobalt chloride paper. One is attached on the lower surface of a leaf by cello-tape [refer experiment iv(a)] and another on wire net placed on a Petridish containing water. Time taken to change the colour of the paper in both the cases is noted and from the above formula the transpiration index can be calculated.

SELECTED QUESTIONS

1. What is transpiration ? How does it differ from evaporation ? Discuss its relation to the absorption of water by roots.

Refer articles 6.1 and 6.2. For the last part refer topic *passive absorption* in Chapter 4, article 4.5.

2. Give an account of the experimental evidence on which theory of the mechanism of stomatal opening and closing is based.

Refer article 6.4

3. Describe the structure and position of leaves in relation to transpiration.

Refer topic *internal factors* in article 6.5

4. Discuss critically the factors affecting the rate of transpiration.

Refer article 6.5

5. Distinguish between evaporation and transpiration. What is transpiration coefficient ?

Give an account of the structure and function of stomata in regulating transpiration.

Refer article 6.2 and for transpiration coefficient refer foot note of experiment (ii) article 6.8. For the last part of the question refer topic *mechanism of transpiration* in article 6.4

6. Discuss the significance of transpiration.

Refer article 6.6

7. Discuss critically transpiration is 'a necessary evil'.

Refer article 6.6

8. What do you mean by guttation ? Explain the mechanism of guttation in plants.

Refer topic *guttation and physiology of guttation* in article 6.7

9. Give an account of the phenomenon of exudation and guttation. Discuss briefly the mechanism and the significance of the processes.

Refer article 6.7

While studying the chemical breakdown of foodstuff van Helmont in the early part of the seventeenth century suggested that the chemical transformation of food stuffs was caused by the "ferments" (latin *fermentare* means to agitate). Gradually with the advancement of science additional evidences were accumulated and in 1817 Davis and others showed that many of the chemical reactions like decomposition of H_2O_2 were accelerated by the presence of certain metals in the reaction. This type of chemical behaviour has been termed as "catalysis" (greek *katalysis* means dissolution) by Berzelius in 1836. Subsequently, with the rapid development of organic chemistry, particularly when information regarding the chemical constituents of the living organisms was accumulated, there was much difficulty to correlate the term "ferments" with that of catalysis and to avoid this confusion Kuhne in 1878 introduced the term "enzymes" to these ferments which could be extracted from cells (greek *enzymes* means in yeast). Further, Buchner's experiment in 1897 clearly suggests that the catalytic components of the extract from the yeast are enzymes.

7.1 Definition : *Enzymes are the active substances like the catalysts produced by living cells, which can alter the velocity of the chemical reactions without being used up themselves and remain unchanged at the end of the reactions.* Their biological function is the catalysis of the chemical reactions in living organisms. In the light of modern concept enzymes can be defined as specific, catalytically active proteins – simple or conjugated. All enzymes are proteins or protein derivatives varying in molecular weight from 10,000 to 500,000.

The action of enzymes known for a long time specially in case of alcoholic fermentation where the production of ethyl alcohol from sugar by yeast (in which the enzyme *zymase* is present) was noteworthy.

7.2 Enzyme and catalyst : Catalysts are substances which can alter the speed of chemical reaction while themselves remaining unaffected chemically or which may be recovered at the end of reaction. We designate "catalyst" to all substances which speed up the reaction. Many, however, slow down the rate of reactions when these are known as *negative catalysts*. Catalysts are, however, required in a very minute quantity to accelerate the reactions. In many cases the catalysts are specific in their functions i.e. they act only on certain specific substances but not all.

Enzymes likewise have all the characteristics of a catalyst i.e. they can accelerate the rate of chemical reactions without themselves being used up. Like catalysts enzymes are also specific in their function. That is why enzymes are known as *organic catalyst produced in the living body*.

Enzymes and catalysts are apparently identical, although there are certain differences. In the process of enzymatic reactions a fraction of enzyme molecules is lost or inactivated due to numerous side reactions in a cell where some of the enzyme molecules are found to be participating. Further, the rate of the enzymatic reaction in a particular reaction is not proportional as all the enzymes can not freely participate in the reaction due to chain of side reactions and consequently the exact proportion is not maintained throughout the reaction. Enzymes are thermolabile, whereas the catalysts require a fairly high temperature to react.

The inorganic catalyst never disappears during the course of reaction, an enzyme gradually disappears, reappearing at the end of the reaction, though unchanged in activity or in amount.

7.3 Types and naming of enzymes : Enzymes are usually active at the place of their synthesis but occasionally they may diffuse out of a cell and act in the outside medium. The former type of enzyme is called **endoenzyme** or **intercellular enzyme** whereas the latter type is known as **exoenzyme** or **extracellular enzyme**. Majority of the plant enzymes are endoenzymes, whereas exoenzymes are found only in the activity of certain bacteria and fungi and in some insectivorous plants (*Drosera*, *Nepenthes* etc.).

With the gradual development of enzyme chemistry there has been a confusion in its terminology. There are various ways of naming an enzyme. Duclaux (1883) introduced the system of naming an enzyme on the basis of the substrate upon which it acts, followed by the suffix—*-ase*, though there are many exceptions. Thus the enzymes *sucrase* which acts only on sucrose, *cellulase* which acts on cellulose, *proteinase* which acts on protein are the examples of this type. Although quite a large number of enzymes are named on this basis, but still this should not be considered as a general rule as there are many exceptions (e.g, *pepsin*, *emulsin* etc.).

Some enzymes are also named according to the types of reactions they catalyse. Thus the enzymes which are responsible for transfer of phosphate group from one molecule to another are known as *transphosphorylases* and when the enzymes are related to the transfer of the hydrogen from one compound to another they are known as *dehydrogenases*.

There is another group of enzymes which are named both on the basis of nature of substrate and nature of chemical reactions. Thus the enzymes *pyruvic carboxylase* and *phosphoglyceraldehyde dehydrogenase* are the examples of third type. Here the first enzyme reacts on pyruvic acid when carbon dioxide is released in the reaction and

the second enzyme reacts on phosphoglyceraldehyde releasing hydrogen from it.

7.4 Chemical nature of enzymes : Difficulty in isolating the enzymes in pure form posed a handicap in understanding their chemical nature. Willstätter and Stoll proposed the 'carrier theory' according to which the enzymes were believed to be carried by some colloidal carrier of high molecular weight which were not necessarily proteins. However, Sumner (1926) obtained the enzyme *urease* in crystalline form from Jackbean meal and showed it to be protein in nature. Since then, in every known case, the pure enzyme has been identified as a protein—simple or conjugated. The enzymes which have been isolated upto date show the same elemental composition of C, H, N and S as in protein. Some of the enzymes, however, contain small amount of P or some metals like Cu, Fe, Mg, Mn and Zn. Some of the enzymes yield amino acids on hydrolysis. Besides the protein part, certain enzymes also contain a non-protein group or a *prosthetic group* which is only active when it remains associated with protein molecule. This non-protein part has been termed by Bertrand in 1897 as *co-enzyme* (for detail refer article 7.12), the dialysable substance essential for enzymatic activity and the protein portion as *apoenzyme*.¹

So, if the prosthetic or non-protein part is removed from an enzyme, the identity of the enzyme is lost and the remaining protein group is unable to act as enzyme. Many of the metals are co-enzymes and are therefore essential in plant nutrition. It should also be borne in mind that although a number of prosthetic groups may be identical for a number of enzymes, still the activity of the enzymes mainly depends on the protein portion of the enzymes.

Thus, several enzymes may contain the same coenzyme, but because they contain the same protein they are specific in action. As for example, *tyrosinase* and *ascorbic acid oxidase* both contain copper (Cu) as coenzyme yet they act differently, *tyrosinase* acts on amino acid tyrosin whereas *ascorbic acid oxidase* acts on ascorbic acid but not on tyrosin. Iron is an activator constituent of many enzymes e.g. *peroxidase*, *catalase* and *cytochrome oxidase*. Iron here does not form the coenzyme itself, but it forms a complex with a porphyrin which then acts as a coenzyme proper.

Some enzymes are more complex since besides protein and coenzyme they contain an activator metal. In the absence of either the coenzyme or metal ion, the protein component is inactive. Thus the enzyme *carboxylase* contain thiamin phosphate as a coenzyme and magnesium as the metal activator. In these cases the coenzymes are usually some complex organic compounds.

¹ According to Euler there are two distinguishable parts of an enzyme : (i) *apoenzyme*—the colloidal, thermolabile protein portion and (ii) *co-enzyme*—dialysable, thermostable part, these two constitute the **holoenzyme**.

Another specific Mn enzyme is *malic dehydrogenase* ; Zn enzymes are *alcohol dehydrogenase*, *carbonic anhydrase* ; Mo enzymes are *nitrate reductase* and *xanthine oxidase*. In the absence of the particular micronutrient ion these enzymes are completely inert and inactive.

Zymogens are the enzyme precursors sometime present in the cell. They, however, remain inactive and can be converted into an active enzyme by the activity of another kind of substances known as *kinases*—widely present in the plant cell whose mode of action is still obscure.

7.5 Properties of enzymes :

(i) *Catalytic properties*—Like catalysts enzymes accelerate the reactions but remain unchanged in mass and in chemical composition at the end of the reaction. The effect of the enzymes can be brought about by a very minute quantity of substance as catalysts do. Like catalysts enzymes are also governed by the laws of thermodynamics in the reacting system.

(ii) *Solubility*—Enzymes are soluble in water, alcohol, saline and also in dilute glycerine.

(iii) *Specificity*—Almost all enzymes are specific in their action i.e. particular enzyme can act only upon certain substrate or a group of substrates. Thus *sucrase* reacts only on sucrose and no other sugars, *lipase* only on lipids (fats), *oxidases* brings about oxidation with the help of atmospheric oxygen. Each substrate is reacted by its own specific enzymes. This means that there should be separate enzymes for separate substances. But in practice, this rule does not hold good in every case as a particular enzyme can react on all substances which have the same molecular configuration. Thus all glycosides are more or less similar in their chemical configuration. So, they are acted on by only one kind of enzyme—*emulsin*.

Four types of enzyme specificity can be distinguished :

(a) *Absolute specificity* : Where the enzyme can catalyse the breakdown of only one substrate e.g. hydrolysis of urea by *urease*.

(b) *Absolute group specificity* : The enzyme can act on only one organic group e.g. action of *alcohol dehydrogenase* on alcohols.

(c) *Relative group specificity* : Where the enzyme can act on more than one organic group e.g. *trypsin* which can act both as *peptidase* and *esterase*.

(d) *Stereochemical or optical specificity* : Where the enzyme exhibits the capacity to distinguish between optical isomers of a given substrate, e.g. most of the *protease* enzymes are specific for l-amino acids or an l-amino acid oxidase will act only on l-amino acid and not on d-amino acids.

In nature, true specific enzymes are very rare ; the best example of this type is *urease* and *cytochrome oxidase*. The former acts only of urea and latter on the cytochrome and no other substances.

(iii) *Reversibility in action*—Like true catalysts enzymes accelerate the reaction in either directions if optimum energy is available. In principle, all enzyme-catalysed reactions are thermodynamically reversible; in some cases, however, the reaction proceeds so far in one direction that it is impossible to perform the reverse reaction. The direction in which the reaction will proceed depends on a number of internal factors of the cells. Thus, the enzyme *lipase* can bring about the synthesis of fats from fatty acids and glycerol under certain condition of the cell which, however, might be reversed due to certain favourable change in the reacting system consequently breaking fats in simpler substances like fatty acids and glycerol by the same enzyme.

(iv) *Sensitivity of enzymes*—Enzymes are very much sensitive to heat and *pH*. With a few exceptions the enzymatic reactions take place at a *pH* nearing neutrality and at a temperature between 20°C–40°C.

Rise of temperature will, therefore, have an effect of increasing the activity of enzyme but high temperature decreases the enzymatic activity due to destruction of enzymes. The most optimum temperature for the enzymatic activity lies between 30°C and 40°C, below or above which there is a decrease instead of increase in the enzymatic reactions. Most of the enzymes are found to be inactivated at about 50°C and above 60°C the enzymes are found to be destroyed. Some enzymes (enzymes of dry seeds), however, can withstand a temperature as high as 100°C. At low temperature (below or nearly the freezing point) enzymes are inactivated rather than destroyed.

Enzymes are also very much sensitive to *pH* and any change (decrease or increase) in *pH* will cause a decrease in the activity of the enzymes. For example, the enzyme *pepsin* can accelerate the reaction in a slightly acidic medium, where as *trypsin* requires an alkaline medium for its activity.

Enzymes are heat labile and are quite unstable in nature. They are inactivated or destroyed by long exposure of light of shorter wavelengths (i.e. UV)

(v) *Colloidal properties*—Like colloidal particles, enzymes that have been so far isolated are molecules of large dimensions and they fall within the range which characterises the particles of the colloidal system. For their large size, the enzymes can diffuse but very slowly and are therefore easily separable from diffusible substances by dialysis.

The sensitivity of the enzymes to heat is due to their colloidal properties. They are coagulated at high temperature.

7.6 Occurrence and distribution of enzymes: Enzymes are present in all living cells although their amount varies considerably. Some of the enzymes concerned with respiration are universally present in all living cells, other enzymes, however, are restricted to certain zones or tissues of the plant body.

Germinating seeds are richest in enzymes. Usually the substrate and the enzymes are present in the same cell, though the activity of the enzymes within the cell depends on a number of factors within the cell. It is also true that the increased accumulation of the substrate within a cell shows a relative increase in the corresponding enzymes in the cell and *vice versa*.

Enzymes are also present in the cells of fungi and bacteria.

7.7 Mechanism of enzyme action : It is now generally agreed that in metabolic processes the substrate molecule must come in contact with the specific enzyme to ensure an enzymatic reaction. This results in deformation in the bonds of the substrate molecule, thus accelerating its reaction. The activity of the enzymes is very much analogous to a complicated lock. When the substrate molecule has a specialized configuration, so as to fit the enzyme molecule, the two can work together like that of a key to a lock. This is known as 'lock and key' system of enzymatic reaction which is shown in Fig. 7.1. This hypothesis was originally proposed by Fischer in 1894.

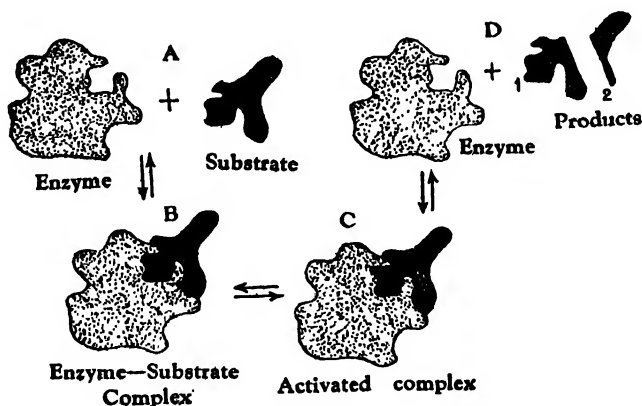
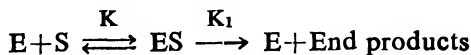


Fig. 7.1 The formation of enzyme-substrate complex.*

The union of substrate with the enzyme is a very specific process i.e. each enzyme has a particular structural configuration with certain regions where the enzymes can join with the substrate. Thus the enzyme-substrate reaction can be written as :



Where E is the enzyme, S is the substrate, ES is the enzyme-substrate complex, K is the rate of the combination of E and S to form ES, and K_1 is the velocity constant of the chemical reaction which gives free energy and end products.

Michaelis and Menten (1931), advanced the *enzyme-substrate complex theory* to explain enzyme action. According to them,

"enzymes were able to act as catalysts because they combined with their substrates—essentially the same principle as Oswald's law of chemical catalysis." Moreover, the activation energy was lower for the enzyme-substrate complex than for the substrate without the enzyme. This ES complex subsequently breaks down to form the end product and liberate free enzyme.

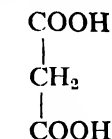
The *enzyme-substrate complex* theory is well supported. There are at least three lines of evidence to support the theory :

(a) The first comes from Keilin's study on the enzyme *peroxidase*. This enzyme catalyses the formation of water from hydrogen peroxide, but can take place only when necessary hydrogen is supplied by a hydrogen donor.

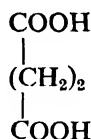


Spectrophotometric analysis of the enzyme peroxidase shows well defined bands at 498, 548, 583 and 645m μ , but on addition of H₂O₂ (without any hydrogen donor) there are only two absorption bands at 530 and 561 m μ , suggesting a reaction between the enzyme and the substrate. On addition of a hydrogen donor the original spectrum is again obtained.

(b) The phenomenon of "competitive inhibition" also support the enzyme-substrate interaction theory. This can be illustrated by the inhibition of *succinic dehydrogenase* by malonic acid. Here an increase in the substrate concentration is simultaneously reflected in a decrease of the percentage of inhibition. The similarity in molecular structure of succinic and malonic acids allows them to enter into combination with the enzyme



Malonic acid

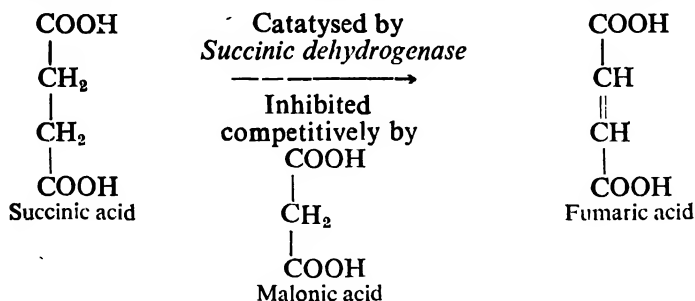


Succinic acid

It has been contended that "the enzyme-inhibitor complex is stable, so that at low enzyme concentration of succinate, malonate is able to combine with the enzyme and preclude the succinate from combining. But at high succinate concentration, the latter is able to compete successfully with malonate for suitable positions on the enzyme's surface"

(c) The third line of evidence comes from the study of the kinetics of enzyme reaction under a wide range of conditions. It has been possible to predict the enzyme kinetics (Haldane, 1930) and calculate the relationship between the velocity of reaction and substrate concentration. It has been subsequently found from carefully conducted experiments that there is a close correlation between the predicted and actual values.

It is evident from the above that the formation of the enzyme-substrate complex must depend on the chemical configuration of the enzymes and substrate so as to fit together. The activity of the enzymes and substrate can also be illustrated by the process known as *competitive inhibition*. The best example of this phenomenon can



be exhibited by the activity of *succinic dehydrogenase* which catalyzes the oxidation of succinic acid. This activity of *succinic dehydrogenase* can be retarded by malonic acid. Experiments show that since the chemical structure of malonic acid closely resembles that of succinic acid, it is apparently attached with the enzyme in a position that would normally be filled up by succinic acid and therefore it competes with succinic acid in reducing the effectiveness of the enzyme.

This enzyme-inhibitor complex is stable and therefore the more enzyme-inhibitor complex is formed, the more the enzymes are removed from their catalytic role; the greater is the reduction in the rate of enzymatic reactions. The rate of union of the inhibitor with the enzyme depends on the concentration of the substrate. If there is an excess of substrate, the inhibitor can not compete and so less inactivity of the enzymes will be observed.

7.8 Classification of enzymes—The classification of enzymes is very difficult. New ideas in enzyme chemistry have altered our view considerably and changed the position of certain enzymes from the systematic classification. Haldane (1930) classified all the C-N linkage hydrolysing enzymes together, but others separate urease from the enzymes *pepsin*, *trypsin* etc. which also break this C-N linkage.

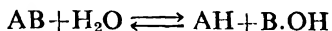
The difficulty in the classification of the enzymes is that, most of the catalytic activities are associated with enzyme preparation of uncertain homogeneity. The rational classification of the enzymes on the basis of specificity is not tenable, but it is customary to classify the enzymes on the basis of reactions they catalyse rather than the nature of the enzyme. The outlines to follow are prepared mainly with the idea of bringing together some of the important information about typical enzymes of various classes. The classification given

here is not at all complete and is simplified by the omission of many synonyms and enzymes of doubtful occurrence.

For practical purposes, enzymes can be conveniently classified into the following groups :

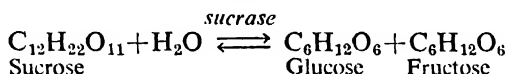
- (i) Hydrolases
- (ii) Splitting enzymes
- (iii) Transferases
- (iv) Isomerases
- (v) Oxidation-reduction
 - (a) Dehydrogenases
 - (b) Oxidases

(1) **HYDROLASES** :—It is a group of enzymes which causes hydrolysis of the substrate. It always involves the use of one molecule of water and the break down of the substrate takes place according to :



The important hydrolases are the *carbohydrases*, *lipases*, *proteases* etc. The main function of these enzymes is to render insoluble reserve food matters into simpler form.

(a) *Carbohydrases*¹—These are the enzymes which cause the hydrolysis of carbohydrate e.g. *sucrase*² causes the hydrolysis of sucrose into glucose and fructose according to



There is another enzyme *maltase*, specially adapted to the hydrolysis of maltose to two molecules of glucose. The best known polysaccharidase is *amylase*, which causes hydrolysis of starch to maltose and glucose.

Among the known amylases there are two broad groups : α - and β -amylases (Hopkins, 1946).

β -amylases rapidly hydrolyse the amylose fraction of starch to maltose. These enzymes attack polysaccharides from the non-reducing end of the chain, cleaving alternate α -glycosidic bonds and hydrolysing of maltose units. Thus the reaction can be complete for a straight chain amylose, but with the branched chain amylopectin the enzymatic reaction stops at the point of branching.

In case of α -amylases on the other hand, the rate of appearance of maltose is very slow and they attack on the glycosidic linkage in the

¹ They are also known as *glycosidases* as they catalyze the hydrolysis of glycosidic bonds (Pigman, 1943).

² It is also known as *invertase* since this hydrolysis of sucrose to glucose and fructose leads to change in optical rotation of the reaction mixture (Neuberg, et al 1950).

interior of the chain of a polysaccharide with the formation of oligosaccharides which are cleaved slowly to maltose and glucose.

There is another amylase known as R-enzyme (Hobson, 1951 ; Peat, 1954) which has been isolated from a number of plants. In some of its properties like its action on branch point in amylopectin molecule, it resembles β -amylases.

(b) *Proteolytic enzymes*—These are the enzymes which cause the hydrolysis of protein and its derivatives. Proteolytic enzymes are very much allied with the enzymes found in the gastro-intestinal tract of mammals. The break down of protein to simpler substances (amino acids) also takes place in the following line.

Protein \rightleftharpoons Proteoses \rightleftharpoons Peptones \rightleftharpoons Polypeptides \rightleftharpoons Dipeptides \rightleftharpoons Amino acids

where the types of enzymes responsible for breakdown of protein upto polypeptide are known as *proteases* and the enzymes which favour further breakdown of polypeptide to amino acids are known as *peptidases*.

Pepsin, *trypsin* and *erepsin* are the important proteolytic enzymes in plants.

Pepsin causes the degradation of almost all proteins upto polypeptides but not of protamines or keratins. The optimum pH for its action on protein varies on the nature of the proteins and is found to be near about 2.

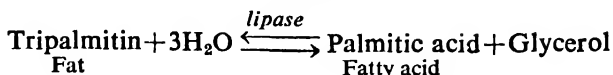
Trypsin, however, attacks proteins in optimal pH near 8, although some activity may be demonstrated at pH values as low as 6. Like pepsin it also acts at CO-NH linkages in synthetic structure and also directs the hydrolysis of protein upto polypeptides, dipeptides and even in some cases upto certain amino acids. It also hydrolyses protamines.

Erepsin, like trypsin can be effective at pH near about 8. It usually hydrolyses the later part of protein degradation (i.e., polypeptide to amino acid).

The modern terminology for the proteolytic enzymes is to designate them as *endopeptidases* and *exopeptidases* when an enzyme attacks peptide bonds in the interior of the peptide chains. Pepsin and trypsin illustrate the activity of endopeptidases. Exopeptidases are also specific in action. They attack a polypeptide and the result is the production of free amino acids.

The best known peptidase is carboxypeptidase which is the best example of exopeptidases. The other two exopeptidases are aminopeptidase and dipeptidase. The function of exopeptidases is very much correlated with erepsin. The carboxypeptidases attack peptides from the carboxyl end of the chain. Amino peptidases attack on the free amino group. Dipeptidase, however, causes a hydrolysis of a peptide link in a dipeptide.

(c) *Lipases*—They usually react with the lipids (fats) and renders them soluble into fatty acids and glycerol.



Lipases are usually found in the seeds of castor, bean, soybean etc. and cause hydrolysis of the stored fats and oils into simpler forms.

Glyceryl esters of fatty acids (neutral fats) are readily hydrolyzed by lipases to fatty acids and glycerol. Simpler esters like methyl butyrate are attacked very slowly by the lipases. Esterases, however, have little or no activity towards neutral fats. The breakdown of triglyceride by lipases is given below.

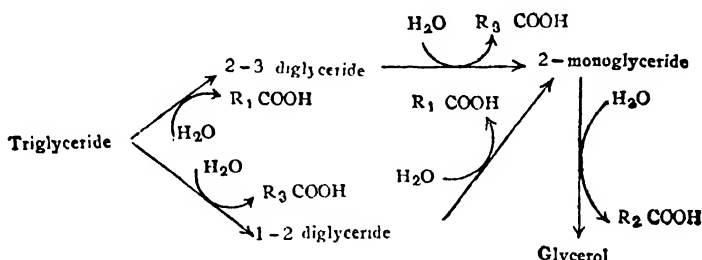
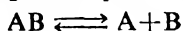


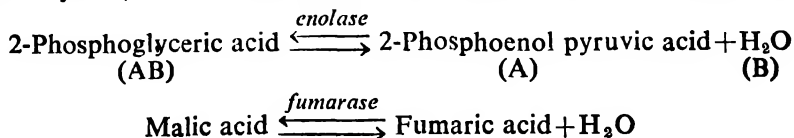
Fig. 7.2 Probable reaction sequence in the complete hydrolysis of triglyceride by lipases.

(2) **SPLITTING ENZYMES**—The enzymes which cause the substrate molecule to split up into two different components are known as *splitting enzymes*. The general plan of the enzymatic reaction :

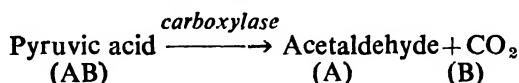


The reverse reaction ($A + B \rightarrow AB$) is of very rare occurrence in plants. When, however, it occurs, the enzymes are known as the 'adding enzymes' as the substrates are added together to form a single compound. The splitting enzymes can be categorically divided into the following groups on the basis of the nature of the end products.

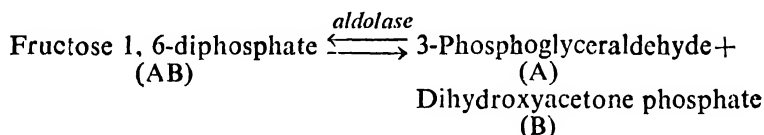
(i) *When one of the end products is water*—The most important examples of such enzymes which cause the formation of one molecule of water as one of its products are *enolase* and *fumarase*. The former being used in the conversion of 2-phosphoglyceric acid to 2-phosphoenol pyruvic acid in the later stage of glycolysis (respiration) and the latter is used in the conversion of malic acid to fumaric acid in the Krebs cycle (aerobic respiration). The overall chemical changes are,



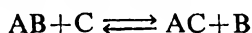
(ii) *When one of the end products is carbon dioxide*—The best example of such an enzyme is *carboxylase* (better called as *pyruvic decarboxylase*) which causes the conversion of pyruvic acid to acetaldehyde and carbon dioxide. It is the initial stage of anaerobic breakdown of pyruvic acid. The reaction is as follows :



(iii) *When two different end products other than H₂O and CO₂ are formed*—The enzyme which causes the conversion of a substrate to two different substances, of which neither is water or carbon dioxide, is termed as *aldolase*. It takes part in one of the most important reactions in the respiration, where fructose 1, 6-diphosphate is converted to equivalent amount of 3-phosphoglyceraldehyde and dihydroxyacetone phosphate.

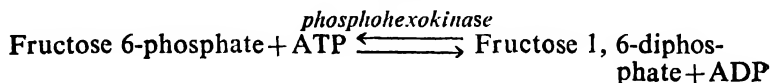
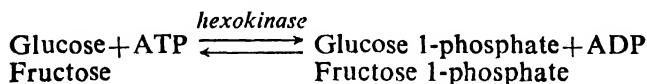


(3) *TRANSFERRASES*—The enzymes which cause the transfer of a part or entire group of one molecule to another are known as *transferases*. The general plan of the reaction

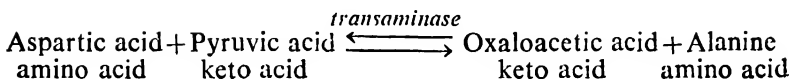
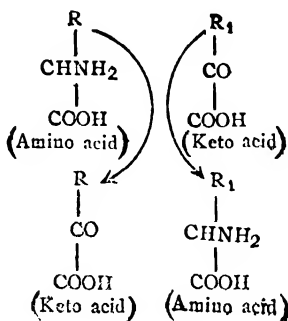
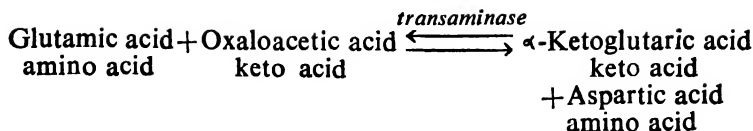


The transferase enzymes are of two types :

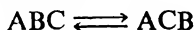
(i) *Transphosphorylases*—When the enzyme causes the transfer of phosphate group from one molecule to another, it is known as *transphosphorylase*. *Hexokinase* and *phosphohexokinase* are the important transphosphorylase enzymes in plants. In both the cases the hexose sugar reacts with adenosine triphosphate (ATP), where one of the terminal high energy phosphate groups is transferred from ATP to sugars in the process of respiration.



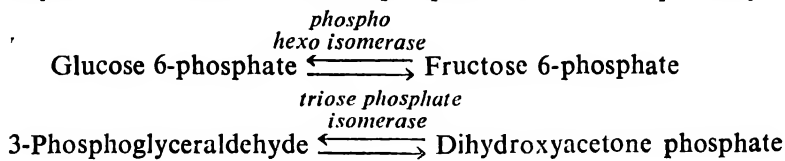
(ii) *Transaminases*—These involve the transfer of amino group (—NH₂) from one molecule to another in the synthesis of amino acids in nitrogen metabolism. The enzymes are capable of catalyzing the transfer of amino group between amino acids and keto acids. The general plan of this type of reaction is given below.



(4) ISOMERASES—They involve the isomeric changes in their substrate from one position to another within the same molecule. Thus

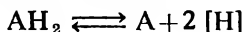


This enzyme plays an important role in the respiration process (glycolysis) in converting glucose 6-phosphate to fructose 6-phosphate and 3-phosphoglyceraldehyde to dihydroxyacetone phosphate by *phosphohexo isomerase* and *triose phosphate isomerase* respectively.

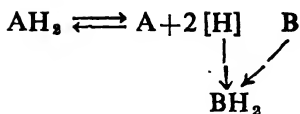


(5) OXIDATION REDUCTION :

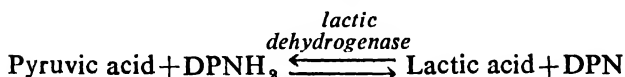
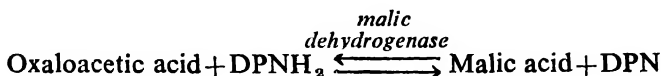
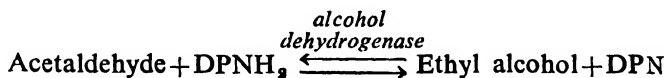
(a) DEHYDROGENASES—They involve catalysis or dehydrogenation by removing not only the electrons but also hydrogen from the metabolites. They therefore cause oxidation of the substrate. The general plan of such a reaction.



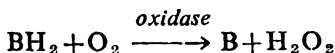
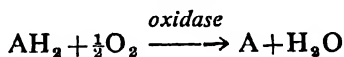
A co-enzyme is always necessary to act as hydrogen acceptor in the reaction. This enzyme therefore catalyzes oxidation-reduction reactions in plants. 'A' is oxidised by dehydrogenation. 'B' is the hydrogen acceptor (co-enzyme) and itself being reduced and the enzyme is a *dehydrogenase*.



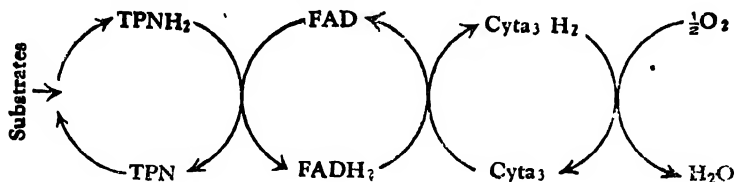
The most important dehydrogenase enzymes are *alcohol dehydrogenase*, *malic dehydrogenase*, *lactic dehydrogenase* etc.



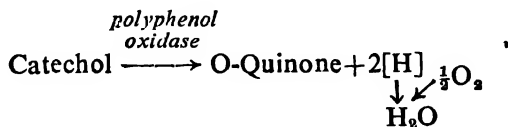
(b) **OXIDASES**—The enzymes that catalyse the transfer of electrons or hydrogen to molecular oxygen are termed as *oxidases*. The oxidases are related in many respects to enzymes that catalyse the oxidation-reduction reactions involving hydrogen peroxide (H_2O_2).

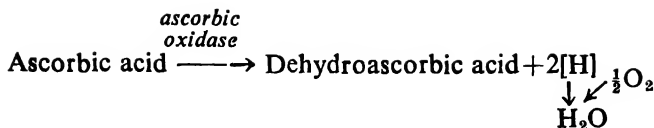


One of the most important *oxidases* in plants is *cytochrome oxidase*. In plants, cytochrome *c* is involved in affecting the electron transport from flavo-adenine dinucleotide (FAD). The reduced cytochrome then passes the electron to the molecular oxygen to give rise to water (refer Chapter 1, article 1.8). The general plan of the oxidation-reduction process in plants is as follows :



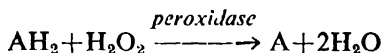
The other plant oxidases are *polyphenol oxidase* (or *tyrosinase* or *catechol oxidase*), *ascorbic oxidase* etc. which cause the oxidation of catechol to o-quinone and ascorbic acid to dehydroascorbic acid respectively.



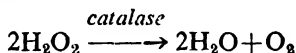


If the oxidase enzymes are involved in the formation of H_2O_2 , they immediately react with *peroxidases*¹ or *catalases*¹ to give rise to water again, as H_2O_2 is toxic to the living system.

The physiological function of the peroxidases is not clear. These enzymes catalyse the oxidation of the metabolites by means of H_2O_2 produced in the direct reaction. Thus the type reaction catalysed by this enzyme is



The best known of the reactions catalysed by the catalases is the decomposition of H_2O_2 .



Enzymes have long been named by the trivial name they possess. Mostly enzymes have been named according to the reactions they catalyzed simply by adding *-ase* in the suffix. Sometimes they have been named with their generic name since they catalyze similar reactions. But with a rapid growth in enzymology during the last several years, difficulties arose in terminology. And since there was no general agreement on nomenclature, same name have been given to different enzymes, different names were given to the same enzyme and similar name have been given to enzymes of different types. Subsequently an International Commission on Enzymes was formed (1961) and they devised a complete and complex system for naming, classifying and coding enzymes systematically. According to this classification enzymes were divided into six general groups :

I OXIDOREDUCTASES

These are the enzymes which catalyze oxidation-reduction (redox) reactions. The so called trivial names of the enzymes *dehydrogenases*, *oxidases*, *oxygenases* and *peroxidases* are included in this division. They transfer electrons and hydrogen ions.

II TRANSFERASES

Transferases catalyze the transfer of a group of atoms from one molecule to another. *Transaminase*, *kinase*, *transphosphorylase*,

¹ It has been found (Keilin and Hartree, 1955) that catalases and peroxidases are more similar in their mode of action than it had been thought previously. For this reason these two enzymes have been placed in a single group termed "hydroperoxidases".

Table 3
General scheme of classification of enzyme with their relative importance in plant metabolism.

Type of enzyme	Type reaction	Example	Reaction	Importance in plant metabolism
1. Hydrolases	$AB + H_2O \rightleftharpoons AH + BOH$	Sucrase Maltase Amylase Endopeptidase Exopeptidase Lipase	Sucrose \rightleftharpoons Glucose + Fructose Maltose \rightleftharpoons 2 Glucose Starch \rightleftharpoons Maltose Protein \rightleftharpoons Polypeptides (\rightleftharpoons Amino acids) Polypeptides \rightleftharpoons Amino acids Fats \rightleftharpoons Fatty acids + Glycerol	Main role in converting insoluble reserve food materials into soluble forms which are utilized during germination of seeds. Peptidases also play an important role in the extracellular digestion by insectivorous plants.
2. Splitting	$AB \rightleftharpoons A + B$	Enolase Fumarase Carboxylase Aldolase	Phosphoglyceric acid \rightleftharpoons Enol-pyruvic acid + H_2O Malic acid \rightleftharpoons Fumaric acid + H_2O Pyruvic acid \rightleftharpoons Acetaldehyde + CO_2 Fructose - 1 - 6(2P) \rightleftharpoons Phospho-glyceraldehyde + Dihydroxy-3-carbon compound (P)	It plays an important role in the later stage of glycolysis (respiration), where due to intramolecular change free energy is converted into high energy phosphate bond. An important stage of the Krebs cycle. It is the first stage of anaerobic respiration in reducing acid to aldehyde. Play a key role in glycolysis, where 6-carbon compound splits into 2-molecules of 3-carbon compounds.

Type of enzyme	Type reaction	Example	Reaction	Importance in plant metabolism
3. Transferases	$AB + C \rightleftharpoons AC + B$	Hexokinase Phosphohexokinase Transaminase	$\left\{ \begin{array}{l} \text{Glucose} + \text{ATP} \rightleftharpoons \text{Glucose-1-(P)} + \text{ADP} \\ \text{Fructose} + \text{ATP} \rightleftharpoons \text{Fructose-1-(P)} + \text{ADP} \\ \text{Fructose-6(P)} + \text{ATP} \rightleftharpoons \text{Fructose-1-6(2P)} + \text{ADP} \\ \text{Aspartic Acid} + \text{Pyruvic acid} \rightleftharpoons \text{Oxaloacetic acid} + \text{Alanine} \end{array} \right.$	<p>Play an important role in the transference of terminal high energy phosphate group of ATP to hexose sugars in raising its free energy level prior to respiration.</p> <p>Capable of catalysing the transference of amino groups between amino and keto acids during amino acid synthesis in plants.</p>
4. Isomerases	$ABC \rightleftharpoons ACB$	Phosphohexo-isomerase Triose phosphate isomerase	$\begin{array}{l} \text{Glucose-6(P)} \rightleftharpoons \text{Fructose-6(P)} \\ \text{Phosphoglyceraldehyde} \rightleftharpoons \text{Dihydroxyacetone phosphate} \end{array}$	They play an important role in the isomeric conversion of several substrates during glycolysis (respiration).
5. Dehydro-genases	$\begin{array}{l} \text{AH}_2 \rightleftharpoons \text{A} + 2[\text{H}] \\ \text{Or} \\ \text{AH}_2 + \text{B} \rightleftharpoons \text{A} + \text{BH}_2 \end{array}$	Succinic dehydrogenase Alcohol dehydro-genase	$\begin{array}{l} \text{Succinic acid} \rightleftharpoons \text{Fumaric acid} + 2[\text{H}] \\ \text{Acetaldehyde} + \text{DPNH}_2 \rightleftharpoons \text{Ethyl alcohol} + \text{DPN} \end{array}$	Main importance in the oxidation of the substrate by removing hydrogen and transferring it to a carrier molecule leading to the synthesis of ATP molecule in Krebs cycle. Playing an important role in the anaerobic respiration in converting aldehyde to alcohol.
6. Oxidases	$\begin{array}{l} \text{AH}_2 + \frac{1}{2}\text{O}_2 \rightleftharpoons \text{A} + \text{H}_2\text{O} \\ \text{Or} \\ \text{BH}_2 + \text{O}_2 \rightleftharpoons \text{B} + \text{H}_2\text{O}_2 \end{array}$	Polyphenol oxidase or Tyrosinase Ascorbic oxidase Cytochrome oxidase	$\begin{array}{l} \text{Catechol} + \frac{1}{2}\text{O}_2 \rightleftharpoons \text{O-Quinones} + \text{H}_2\text{O} \\ \text{Ascorbic acid} + \frac{1}{2}\text{O}_2 \rightleftharpoons \text{Dehydro-ascorbic acid} + \text{H}_2\text{O} \\ \text{Reduced cytochrome} + \frac{1}{2}\text{O}_2 \rightleftharpoons \text{Cytochrome} + \text{H}_2\text{O} \end{array}$	<p>Its main role is browning of the cut surfaces of apples due to oxidation of catechol.</p> <p>These enzymes play an important role in transferring hydrogen from the substrate molecules to molecular oxygen which are incidentally related with the synthesis of ATP molecules.</p>

transacetylases are the trivial names of the enzymes included in this group. The enzymes of this division usually transfer carbon, aldehydic or ketonic residues, sulphur-containing, phosphorus-containing, nitrogenous and glycosyl groups.

III HYDROLASES

Hydrolases catalyze the hydrolysis of a complex molecule into two components reacting with water across the bond which is cleaved. The enzymes are usually named on the basis of substrate they hydrolyse. Thus the correct terminology of *lipase* (trivial name) would be "*glycerol ester hydrolase*". The other hydrolase enzymes are *peptidases*, *phosphatases* and *amidases*.

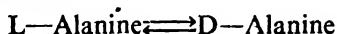
IV LYASES

These enzymes catalyze either the removal of a group of atoms from their substrate leaving double bond or add groups to double bond without hydrolysis, oxidation or reduction. These enzymes usually act on C—C, C—O, C—N, C—S bonds. Thus *malate hydrolyase* (trivial name *fumarase*), *carboxylyase* (trivial name *decarboxylase*) are the typical example of lyase enzymes.

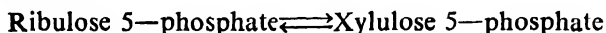
V ISOMERASES

They catalyze the intramolecular rearrangement of atoms in their substrate i.e., they catalyze different types of isomerization. They include a large variety of enzymes :

(a) *Racemase*



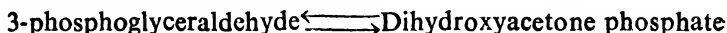
(b) *Epimerases*



(c) *Cis-Trans Isomerase*



(d) *Intramolecular Ketol Isomerases*

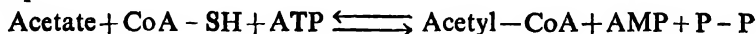


(e) *Intramolecular Transferases or Mutases*



VI LIGASES (SYNTHETASES)

They catalyze the linkage of two molecules coupled with the breakdown of a pyrophosphate bond in ATP or a similar triphosphate. Thus *acetate : COA - SH - ligase* (trivial name *acetic thiokinase*) which catalyze the following reaction is a typical example of this group.



7.9 Factors affecting enzymatic reaction : The presence of enzymes in plant cells not only accelerates or retards the chemical reactions but due to their high specificity they are able to regulate a number of chemical reactions taking place in a cell simultaneously. In other words, enzyme specificity causes an independent control of each reaction.

Each enzymatic reaction, like all reactions is again governed by a number of factors and the influence of all these factors upon enzymatic reactions has been studied *in vitro* in case of higher plants. The study has been made by keeping a purified extract of enzyme on the substrate and maintaining the condition of the reactions. It has been found that temperature, pH, hydration, concentration of the substrate, accumulation of the end products, presence of the inhibitors, accelerators etc. play important roles in the enzyme activity.

(i) *Temperature*—It is one of the most important factors which control effectively the rate of enzymatic reactions. Its effect on the enzyme activity should be studied not only by the degrees of temperature but also by the length of time during which the substrate is reacting at that particular temperature (*time factor*).

At 0°C the rate of an enzyme-catalysed reaction is practically zero. Normally, enzymatic reactions rise with the rise of temperature upto $\pm 40^{\circ}\text{C}$. The increased temperature has got either a direct effect on the reaction system or it may have some effect on the structure of the enzyme. The optimum temperature for an enzymatic reaction lies generally between 30°C and 40°C . There are some enzymes which can withstand a temperature as high as 60°C .

Activity or the rate of the reaction decreases at higher temperature which favours the partial inactivation of the enzymes. Another possible explanation of the enzymatic reactions at higher temperature lies in their reverse reaction, causing an accumulation of the substrate molecules and consequently retarding the reaction rate. At higher temperature the enzymes are destroyed due to protein *denaturation* i.e. due to loss of natural properties.

(ii) *Hydrogen-ion-concentration*—The enzymes are very restricted in their activity by the hydrogen-ion-concentration of the medium in which they are acting. Generally the optimum pH value for the enzymatic activity varies considerably. The direction of enzymatic reaction depends mainly on the pH of the medium provided the other factors are not limiting. Thus pH 7.5 is found to be optimum for the conversion of malic acid to fumaric acid, but for the reverse reaction the optimum pH is about 6.2.

The general range of pH values for the enzymatic activity varies from pH 1.5 to pH 10.0. At higher or lower pH values the enzymes are inactivated, first reversibly and then irreversibly, causing an ultimate decrease in the activity.

Changes in the pH cause denaturation of the enzyme molecule resulting in the decrease of enzymatic activity. Since the proteins

possess many ionic groups, any change in the ionic state of the substrate caused by the change in pH may influence the reaction rate.

(iii) *Concentration of the enzymes*—If there is an excess substrate available and the pH , temperature and other conditions are not limiting then there is a linear relationship between the concentration of the enzymes and the rate of enzymatic reactions i.e. by doubling the amount of enzymes the activity can also be increased. Increasing the enzyme concentration, in fact, increase the number of available active sites, thus increasing the chance of reactive contact between enzyme and substrate.

(iv) *Concentration of the substrate*—Assuming that the concentration of the enzymes in the cell and other conditions are favourable for enzymatic reaction, the increase in the concentration of the substrate causes an increase in the rate of reaction upto certain limiting value, beyond which there is no increase in the rate of reactions. Increase in the substrate concentration causes an increase in the number of reacting molecules in the vicinity of the enzyme's active sites which therefore, increase the rate of an enzyme-catalysed reaction. The increase of substrate molecules in the reaction causes an active accumulation of end products, which until and unless are removed can not accelerate the reaction rate. Further, the excess substrate decreases the water concentration in the medium and which may have indirect effect on enzymatic reaction.

(v) *Concentration of the end products*—Like all chemical reactions, the enzymatic reactions also follow the laws of chemical equilibrium, which means that the active accumulation of the end products will cause a decrease in the reaction rate. The velocity of the enzymatic reactions, therefore, depends on the speed with which the products are removed from the medium. The presence of end products may have an effect in inactivating part of the enzymes thus decreasing the rate of reactions.

(vi) *Hydration*—The amount of water in the medium may have a direct effect on the enzymatic activity. The increased hydration causes an increase in the enzymatic activity. Its effect can easily be demonstrated during germination of seeds. During germination, the activity of the enzymes increases due to increase in the hydration of the tissues.

(vii) *Activators*—There are many substances which when present in the chemical reaction can accelerate or augment the reaction rate considerably. These are known as *activators*. Activators may be general or specific. Solutions of salts or alkali or alkaline earth metals at a very low concentration (3-5%) act as general activators as these can increase the activity of all the enzymes. Co, Mn, Ni, Mg are the specific activators activating only certain enzymes. For detail refer Chapter 12.

(viii) *Inhibitors*—Like activators there are many substances which when present in the reaction decrease the rate of enzymatic reactions. These compounds are known as *inhibitors*. Salts of heavy metals, trichloroacetic acid and cyanide are the examples of inhibitors.

Interaction of enzyme with such a substance leads to an alteration of structure essential to catalytic activity. As a result of this, there is a complete inactivation of the enzyme. Enzyme inhibitions are of two types, **competitive** and **noncompetitive**. In case of competitive inhibition the structural analogs compete with normal substrate molecule. This inhibition can be overcome by increasing the substrate molecule. In case of noncompetitive inhibition, however, the inhibitor reacts with either part of enzyme thus inactivating it or with the enzyme-substrate complex. In the former case it destroys the ability of the enzyme and substrate to interact whereas in the latter case, the inhibitor makes the enzyme-substrate complex inactive.

7.10 Experiments on enzyme activity :

(i) *Action of amylase on starch*—Grind about 50 germinated wheat grains (with seed coat removed) in a mortar with a little quartz sand. Mix the extract with 4 times its volume of distilled water and allow it to stand. After two hours, filter the extract and the filtrate is crude amylase together with other enzymes.

Take 5 ml of this extract from wheat grains in two separate test tubes and heat one tube to boiling. To each tube add 5 ml of starch solution¹ and shake thoroughly. Now test the content of the tubes with I_2 -KI solution² at frequent intervals of time.

Note that the content of the tube boiled previously does not show any change of blue colouration due to inactivity of the enzymes. But the content of the other tube shows gradual change of blue colouration ultimately losing the blue colouration indicating that all starch have been converted to sugar by amylase—extracted from the germinated wheat grains.

(ii) *Effect of pH on amylase activity*—Prepare several buffer solution³ of varying pH values (i.e. pH 3.0, 4.0, 5.0, 6.0 etc.) and take them in small beakers. To each beaker add 5 ml of 0.1% starch solution and 1 ml of amylase solution [refer experiment (i)]. The beakers were then shaken thoroughly. After about 2-3 minutes the content of each beaker is tested with I_2 -KI solution as in experiment (i). Time taken for completion of the reaction in each case is noted (indicated by the loss of blue colour with I_2 -KI solution).

Now plot these results in a curve with the velocity of the reaction as the ordinate and pH values on the abscissa and note the optimum pH at which the amylases are most active.

(iii) *Action of sucrase on sucrose*—Grind 3 g of commercial “dry yeast” to a fine powder and mix with 50 ml of distilled water in a beaker, allow it to stand and then filter. The filtrate is the crude extract of sucrase. Take 25 ml of each tube. One of the tubes is heated to boiling. Now test 5 ml of the content

¹ Starch solution is prepared by dissolving 1 g of soluble starch with 25 ml of distilled water and the paste is now added slowly to 50 ml of boiling water. Rinse the paste with another 25 ml of distilled water and add to boiling water. It gives a 1% starch solution. Dilute 10 ml of this 1% starch solutions to 100 ml with 0.05M KH_2PO_4 after adjusting the phosphate solution to pH 6 with NaOH.

² Dissolve 5 g of KI in 100 ml of distilled water and then add 3 g of crystalline iodine to the solution—then dilute it to 1000 ml.

³ For buffer solutions refer Chapter 1, article 1.11.

from each tube with 5 ml of Benedict's solution and note the amount of cuprous oxide precipitated in each case.

(iv) *Action of lipase on fat*—Remove the seed coat of about 25 germinated castor seeds and grind them in a mortar with little quartz sand and add about 50 ml of 5% NaCl solution. Keep the extract in a stopped jar for about 24 hours and then filter. The filtrate is the crude extract of lipase.

Take a small bottle and add 10 ml of the lipase extract, 9 ml of distilled water, 1 ml of castor oil and 5 ml of 10% gum acacia emulsion. Shake the bottle carefully so that entire mixture is emulsified. A control containing same proportion of water, castor oil and gum acacia (i.e. except lipase extract) is prepared. Now check the pH of the medium by litmus paper. The original solution must be a neutral (as fat digestion to fatty acids results at this pH). Both the bottles were stoppered after adding few drops of toluol and incubate them to about 35°C for 3 days.

At the end of the experiment add 1-2 drops of phenolphthalein solution (indicator) to the solution of the bottle and titrate them with 0.02N NaOH until a faint pink colour remains with continued stirring.

The difference in the two readings obtained after titrating two bottles shows the amount of acid formed by the activity of the enzymes due to break down of fat (palmitin).

Litmus paper can be used as an indicator to show the resulting acid reactions after lipase activity.

(v) *Action of papainases on proteins :*

(a) *Action of bromelin*—Grind and squeeze out the juice from some ripe pineapple tissues. Filter the juice and the filtrate is found to contain bromelin. Take 10 ml of such extract in two test tubes and one of the tubes boiled. Add two small cubes cut from the white of a hard boiled egg to each tube. The first set therefore contains extract and two egg cubes and the second set contains extract which was boiled previously before the cubes of the eggwhite are dropped into it.

Few drops of toluol were added to each tube and place them in an incubator maintained at 37°C for a period of two days.

After two days the sizes of cubes are found to be decreased considerably in the first set but not in the second set as the temperature causes the enzymes of the extract inactive.

(b) *Action of papain*—1 g of commercial papain is mixed thoroughly with 30 ml of distilled water. It is then incubated at 30°C for 1 hour. Filter and the filtrate corresponds to the crude extract of papain.

Repeat experiment (a) using papain instead of bromelin and note the size differences of the eggwhite cubes.

(vi) *Experiment on enzyme specificity*—Extract about 20 ml of amylase from the young germinated wheat [refer experiment (i)]. Take four test tubes and add 5 ml of the extract to each tube. To the first set 10 ml of 1% starch solution, to the second set 10 ml of 3% cane sugar solution, to the third set two drops of castor oil with 10 ml of 1% sodium carbonate and to the last set one or two blocks of white of egg with 10 ml of 0.2% HCl were added.

Now, test first and second sets with Benedict's solution to show the presence of reducing sugar. Test third set for lipase and the fourth set for proteolytic enzymes. It is evident that only the first set exhibits positive tests for reducing sugar as the amylase is specific in nature—acting only on starch and on no other substances.

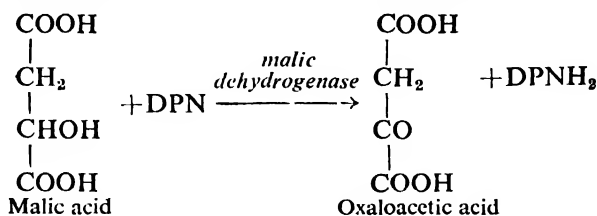
7.11 Isoenzymes or isozymes : When the enzymes have the same function, but present in more than one molecular form within the tissue, these are termed as *isoenzymes* or *isozymes*. Lactic dehydrogenase is a good example of this type of enzyme. In the chicken,

lactic dehydrogenase occurs in two principal forms designated as 'M' (for skeletal *Muscle*) and 'H' (for *Heart muscle*), which appear to be controlled by two separate and independent genes. These two forms are distinguishable on the basis of amino acid composition and physical immunologic and catalytic properties.

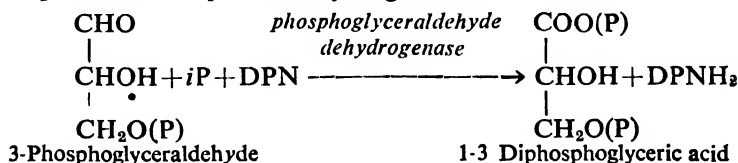
There are altogether five different lactic dehydrogenases which are typically isoenzymes. The structure of lactic dehydrogenase provide a ready explanation for these results. Since lactic dehydrogenase is a tetramer and consists of two subunits designated as 'M' + 'H', the five structurally distinct lactic dehydrogenase are H_4 , H_3M , H_2M_2 , HM_3 and M_4 .

7.12 Co-enzymes : The term "co-enzyme" has been used first by Bertrand (1897) to designate dialyzable substances essential for enzyme activity. Following the early concept of Bertrand, Harden and Young (1904) found that if the extract of an enzyme is dialyzed, activity of the enzyme was lost, but could be restored by the addition of dialyzable material. The protein part of the enzyme is known as *apoenzyme* and the dialyzable non-protein prosthetic group is known as *co-enzyme*. According to Haldane "co-enzyme is a thermostable crystalloid organic substance of fairly high specificity which permits or increases enzyme activity".

Harden and Young recognised a classical co-enzyme from yeast which they referred to as cozymase. This cozymase is also referred to as *co-enzyme I* or *diphosphopyridine nucleotide* abbreviated as DPN. DPN is said to be the vital component and acts as prosthetic group of the dehydrogenase enzyme system which cause the oxidation of the substance by removing two hydrogen atoms. The hydrogen removed from the substrate molecule reduces the co-enzyme. DPN acts as a co-enzyme for a number of dehydrogenases. Thus, *malic dehydrogenase* which causes the conversion of malic acid to oxaloacetic acid



and *phosphoglyceraldehyde dehydrogenase* which cause conversion of 3-phosphoglyceraldehyde to 1-3, diphosphoglyceric acid are the examples of DPN specific dehydrogenase.



Other important examples of co-enzymes are the *co-enzyme II* or *triphosphopyridine nucleotide* abbreviated as TPN¹. Like DPN, the main role of TPN is that they are active with certain specific dehydrogenase which acts to remove hydrogen from the substrate to co-enzyme II (TPN). In contrast to DPN and TPN which serve as intermediate carriers of hydrogen transfer, there are ADP (a phosphate acceptor) and ATP (a phosphate donator) acting in phosphate transfer in living body. Co-enzymes are therefore essential components as intermediate carrier, in certain linked enzymatic transfer reactions.

The following are the other important co-enzymes in plants :

1. *Thiamine pyrophosphate* (TPP) or *Co-carboxylase* was first isolated from yeast. It is the co-enzyme of carboxylase or decarboxylase. This co-enzyme is synthesized from thiamine, sodium pyrophosphate and dehydrated phosphoric acid.

The main role of TPP is in the oxidative decarboxylation of pyruvic acid.

2. *Lipoic acid* or *thioctic acid* has also been isolated from yeast. It also takes part in the oxidative decarboxylation stage between thiamine pyrophosphate and co-enzyme A.

For more details of this co-enzymes refer Chapter 15.

3. *Riboflavin phosphate* was first isolated from bottom yeast. Its association with some specific proteins constitute a number of enzymes e.g. L-amino acid oxidase, cytochrome *c* reductase etc. This co-enzyme is also known as *flavin mononucleotide* (FMN). This enzyme plays an important role in the oxidation-reduction process in plants.

Riboflavin phosphate sometimes contains adenylic acid (adenine ribose phosphate) and thus a dinucleotide structure referred to as flavin adenine dinucleotide (FAD). It is the prosthetic group of a number of flavoprotein enzymes.

4. *Pyridoxal phosphate* is also known as co-decarboxylase when acting as a co-enzyme with amino acid decarboxylase and detransaminase when acting as co-enzyme with amino acid transaminases. So it plays an important role for a variety of enzymes concerned with amino acid metabolism. It also acts with the enzymes like amino acid dehydrases and amino acid desulphhydrases in the deamination of a number of amino acids.

¹ The new names of DPN and TPN are 'nicotinamide adenine dinucleotide' (NAD⁺) and 'nicotinamide adenine dinucleotide phosphate' (NADP⁺). The actual structure of co-enzyme I & II reveals that they are not phosphorylated pyridine. They in fact, contain an analogue of pyridine—namely nicotinic acid amide and phosphate group is removed. The term "nicotinamide" includes a phosphate group, so by using DPN we are incorrectly indicating more phosphate groups than are actually present. The co-enzyme is a dinucleotide. So NAD⁺ for DPN and NADP⁺ for TPN are logical abbreviations. In this text we shall use both DPN, TPN and NAD⁺, NADP⁺ as this changeover is not possible in all cases.

5. *Heme* is another prosthetic group acting with the enzymes like catalase, peroxidases and cytochrome oxidase.

Heme serves as coenzyme of proteins involved in the transfer of oxygen from one site in the organism to another, for enzymes catalyzing a variety of oxidation reactions and for enzymes catalyzing the cleavage of peroxides.

6. *Co-enzyme A* (Co-A) has been isolated by Lipmann (1945) and is found to contain the vitamin-pantothenic acid.

This enzyme contains the most important physiologically active part—sulphydryl group and hence can be written as CoA-SH.

7. *Adenosine monophosphate* (AMP), *adenosine diphosphate* (ADP) or *adenosine triphosphate* (ATP) are co-enzymes which are active in phosphate transfer and transphosphorylation in connection with various specific enzymes.

8. *Co-enzyme Q* has been isolated by Crane and others (1957). It is a crystalline quinone and an integral part of the electron transport system. A large number of different Q co-enzymes have been formed and all these different chemical forms are known as *ubiquinones*. In the electron transport system they usually occupy a position in the chain between cytochrome *b* and FAD.

Besides all these co-enzymes, certain other compounds like ascorbic acid, folic acid, biotin, vitamin B₁₂ and many other compounds also act as co-enzymes.

SELECTED QUESTIONS

1. Define an enzyme. How can it be distinguished from a catalyst.

Refer article 7.1 and 7.2

2. Give an account of the enzymes with special reference to their chemical nature, properties and occurrence.

Refer article 7.4, 7.5 and 7.6

3. Write a critical account about the mechanism of enzyme action in plants.

Refer article 7.7

4. "The concept of enzyme-substrate complex seems so be sufficiently justified"—Discuss the statement in relation to Michaelis constant.

Refer article 7.7

5. Write an essay on the classification of plant enzymes.

Refer article 7.8

6. Write an essay on enzymes with special reference to those concerned in hydrolysis.

Refer topic *hydrolases* in article 7.8

7. What are oxidising-reducing enzymes in plants? Give a critical account of them.

Refer topics *dehydrogenases* and *oxidases* in article 7.8

8. Describe the factors affecting the rate of enzymatic activity. Assess their relative importance.

Refer article 7.9

9. "A prosthetic group may be called a firmly bound co-enzyme"—Discuss the statement critically.

Refer article 7.12

10. Write an essay on enzymes particularly with reference to their importance in plant metabolism.

Refer table 3

11. In what way do enzymes speed up chemical reactions? How is it possible for an enzyme to effect the decomposition of many molecules of its substrate without itself being substantially altered?

Refer article 7.7

12. Write notes on co-enzymes. What do you mean by isoenzymes?

Refer article 7.11 and 7.12

Plant Pigments

Plant pigments are the synthetic products of the plants, formed during the metabolic activities of the cell. Various pigments are found in plants, of which *chlorophylls* are the most important. They represent the green colour of the plants and are always associated with the plastids. Their main role is in the photosynthetic process of plants. Besides, there are the yellowish coloured *carotenoids* which always remain in association with chlorophylls or may be independently dissolved in the plastids. They are never found in the cell sap of the plant. *Anthocyanins* are another group of colouring matters which are always dissolved in the cell sap. They are responsible mainly for the bright colour of the flowers and fruits. Their main role is to attract the insects for pollination and dispersal of seeds.

8.1 Chlorophylls : Leaf chlorophylls exist mainly in two forms named *chlorophyll-a* and *chlorophyll-b* (Willstätter and Stoll, 1913) which are magnesium prophyrin compounds. In addition to chlorophyll-*a* and-*b*, several other closely related compounds have been found to occur in nature. These are designated as *chlorophyll-c*, *chlorophyll-d* and *chlorophyll-e*.

Chlorophyll-a is present in all photosynthesizing plants. *Chlorophyll-b* is found to be present in green algae, bryophytes and pteridophytes. In the brown algae, diatoms and flagellates, *chlorophyll-a* is accompanied by *chlorophyll-c*. In the red algae, *chlorophyll-d* is present together with *chlorophyll-a*. *Chlorophyll-e* is present in 2 genera of Xanthophyta—*Tribonema* and the zoospores of *Vaucheria*. The photosynthetic purple bacteria contain *bacteriochlorophyll*—very much analogous to *chlorophyll-a* but differ from it in having two additional hydrogen atoms and one more oxygen atom and different substitute group in one pyrrole ring. Besides these, *bacterioviridin* is also found in photosynthetic bacteria.

The chlorophyll content of normal green leaves varies between 0.05 and 0.2% of the fresh weight and the ratio of *chlorophyll-a* to *chlorophyll-b* is usually about 2.5.

There is a close correlation between *chlorophyll-b* and starch formation. A *chlorophyll-b* deficient organism usually does not store starch as reserve food. In *Vaucheria*, a *chlorophyll-b* deficient alga, foods are always stored in the form of fat and oil globules and not as starch. This is true for monocotyledons also. Monocotyledons which seldom form starch as reserve food are also found to be somewhat deficient of *chlorophyll-b*. So there is a kind of incompatibility between starch formation and *chlorophyll-b* deficiency.

Chemistry of chlorophylls—Chlorophyll molecules are very complex. Willstätter and Stoll (1913) isolated the pure chlorophyll pigment from green leaves and established that the pigment essentially consists of two major components—chlorophyll-*a* and chlorophyll-*b*. Their molecular formulas show that these are made up of five different kinds of elements. The chemical composition of which is given below :

Chlorophyll-*a*— $C_{55}H_{72}O_5N_4Mg$

Chlorophyll-*b*— $C_{55}H_{70}O_6N_4Mg$

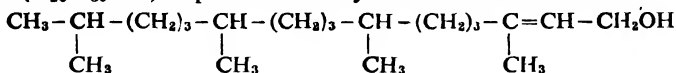
Chlorophyll-*c*—exact structure not fully known, but possibly lacks phytol and ring IV is not reduced.

Chlorophyll-*d*—has a formyl group (CHO) instead of vinyl at I pyrrole ring ($C_{54}H_{70}O_6N_4Mg$).

Bacteriochlorophyll— $C_{55}H_{74}O_6N_4Mg$

Bacterioviridin— $C_{55}H_{72}O_6N_4Mg$

The structure of the chlorophylls was definitely established by Fischer and Breitner (1936). In chlorophyll molecule, the atom of magnesium occupies in the centre of the molecule and surrounded by four nitrogen containing pyrrole nuclei linked by CH bridges. Structurally it is very much similar to the structure of *haeme*, the red pigment of blood. In *haeme* the central position is occupied by iron instead of magnesium. In addition to four pyrrole units, an additional cyclopentane ring is attached to the III pyrrole unit, this ring is absent from the *haeme* pigment. In chlorophyll two extra hydrogen atoms are present in IV pyrrole ring. This pyrrole ring is therefore very susceptible to oxidation and reduction. In the absence of these two hydrogen atoms in IV pyrrole ring, the structure is a *protochlorophyll*. So from *protochlorophyll* to chlorophyll a photo-reduction (i.e. the addition of these two hydrogen in IV pyrrole in light). From IV pyrrole ring there is a long chain alcohol, the *phytol* part of the chlorophyll molecule. When both chlorophylls-*a* and-*b* are hydrolysed, a long chain, optically active aliphatic alcohol called *phytol* ($C_{20}H_{39}OH$) is produced. Phytol has the structure.



Several different degradation products are produced when chlorophyll is treated with acid, alkali or enzymes. Thus, when chlorophyll is treated with weak acid, it is converted into *phaeophytin-a* by the displacement of magnesium by hydrogen atoms. With strong acid the metal is removed to form a compound known as *phaeophorbide-a* which, however, can be dehydrogenated to yield *pheoporphyrin-a* when it is treated with HI. The structural formula of chlorophylls is given below.

The formula in Fig. 8.1 is that of chlorophyll-*a*. In chlorophyll-*b* the methyl group (CH_3) is, however, replaced by aldehyde group

($-\text{CHO}$) decreasing two hydrogen atoms and addition of one oxygen atom to the above molecular formula.

Chlorophyll-*c* is very closely related to chlorophylls except that it does not contain the phytol chain; instead it contains an unidentified chromatophore group. In chlorophyll-*d* the vinyl $\text{CH}=\text{CH}_2$ side chain of I pyrrole ring of chlorophyll-*a* has been replaced by CHO . The chemistry of chlorophyll-*e* is not known definitely.

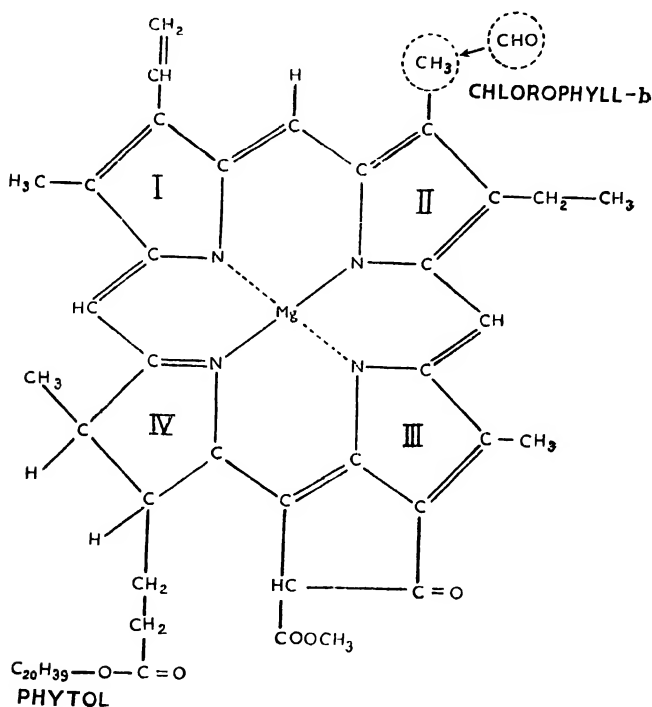


Fig. 8.1 Chemical structure of chlorophyll-*a*. I-IV are four porphyrin rings. The formula for-*b* is the same except that $-\text{CHO}$ group occurs in place of CH_3 group enclosed in the circle.

In case of bacteriochlorophyll the vinyl group ($\text{CH}=\text{CH}_2$) of I pyrrole ring is replaced by an acetyl group ($\text{CO} \cdot \text{CH}_3$) and an additional hydrogenation in C_3 and C_4 of II pyrrole ring. In bacteriochlorophyll therefore both II and IV pyrrole rings are hydrogenated but in chlorophyll it is only in IV pyrrole ring. In bacterioviridin, the vinyl side chain is replaced by hydroxyethyl group ($\text{CH}_2 \cdot \text{CHOH}$). In II pyrrole ring CH_3 is replaced by a *n*-propyl side chain and the carboxymethyl group of cyclopentane ring is eliminated.

Biosynthesis of chlorophylls—Until 1960 very little was known about how an organism synthesized these complex chlorophyll molecules inside the chloroplasts (except blue-green algae which have no chloroplasts).

In 1961, Granick and Mauzerall proposed a scheme (Fig. 8.2) for biosynthesis of chlorophyll-*a*. With the exception of one or two steps, majority of the stages have been clearly investigated. According to Shemin (1956) the early precursors of porphyrin synthesis are glycine and succinyl Co-A, which are considered to be parts of the TCA cycle. These then by decarboxylation form δ -amino-laevulinic acid (ALA) via α -amino β -keto adipic acid through a cycle known as Shemin cycle.

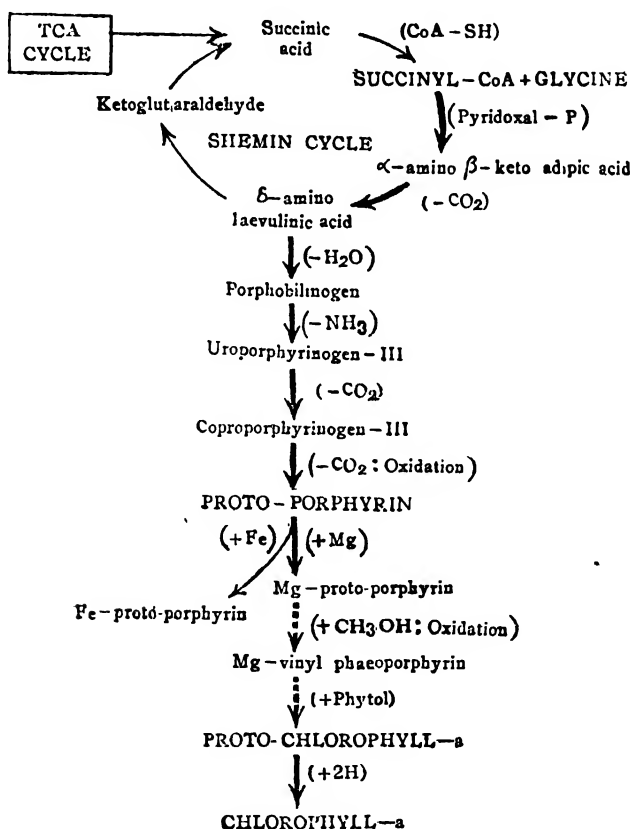
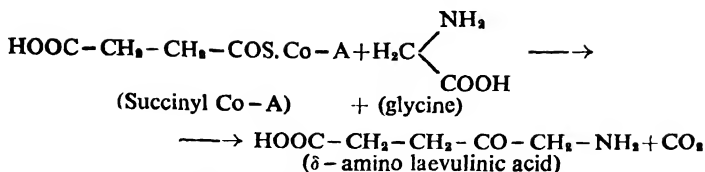
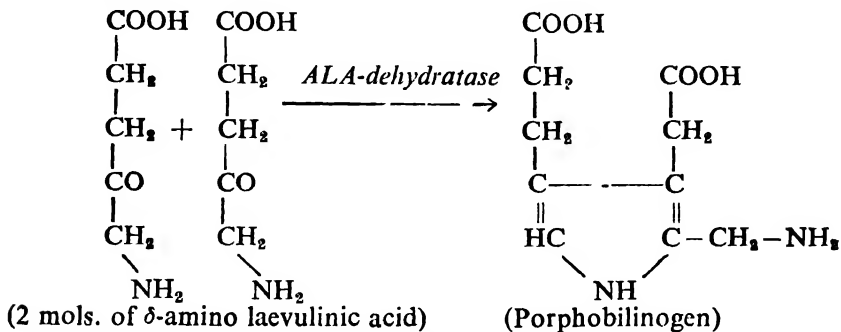


Fig. 8.2 Biosynthesis of chlorophyll-*a*



2 molecules of δ -amino laevulinic acid units head to tail to form the pyrrole derivatives—prophobilinogen (PBG) (Burnham and Lascelles, 1963).



4 molecules of porphobilinogen (PBG) then gives rise to uroporphyrinogen III with the enzyme—*porphobilinogen deaminase* (obtained from spinach chloroplasts and *Rhodospseudomonas spheroids*).

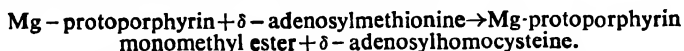


Uroporphyrinogen III then by decarboxylation produces coproporphyrinogen III. Coproporphyrinogen III then form protoporphyrinogen which ultimately oxidised to protoporphyrin IX.



The number of enzymes involved above is not known and there is no information on the oxidative decarboxylation mechanism (Sano and Granick, 1961; Porra and Falk, 1963).

Protoporphyrin IX is the immediate common precursor of chlorophyll and other porphyrins (protohaeme); interaction of Mg in the centre of this molecule produces Mg-protoporphyrin. Mg-protoporphyrin then through a series of interconversions produces chlorophyll. We know very few of the enzymatic steps involved in this transformation and the intermediates.



Mg-protoporphyrin monomethyl ester then converts to Mg-vinylpheoporphyrin a_5 (protophlorophyll). The reduction of this compound to chlorophyll involves reduction of the tetrapyrrole ring and an esterification of this residue by phytol, a long chain alcohol.

The intermediates of these reactions probably never occur in the free state. It should be mentioned that the reactions takes place in higher plants and in some algae only in the presence of light.

Chlorophyll-*b* does not originate from chlorophyll-*a* or by the same process through which chlorophyll-*a* is synthesized. The details are however not known.

Properties of chlorophylls—Chlorophylls are microcrystalline. Chemically they are methyl esters of parent dicarboxylic acid—the *chlorophyllins*.

Chlorophylls are insoluble in water but soluble in a number of organic solvents like alcohol, chloroform, acetone, benzene, ether, carbon bisulphide etc. and quite insoluble in petroleum. When they are in solution chlorophyll-*a* gives a typical blue-green colouration and chlorophyll-*b* shows a pale green colouration and when viewed as a whole it shows a green colour.

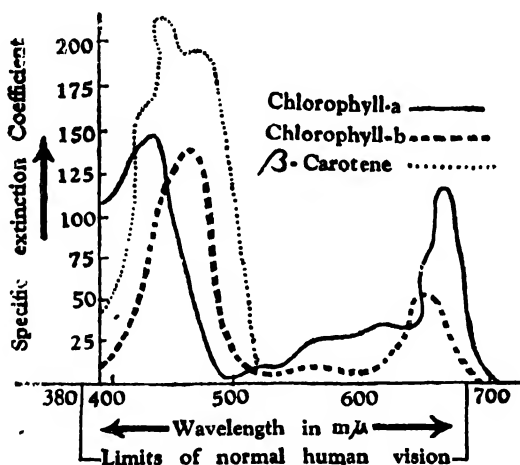


Fig. 8.3 Showing the patterns of energy absorption among chlorophylls and β -carotene.

Chlorophylls exhibit the property of fluorescence, which means, the property of absorption of radiation by a substance and its re-emission at a longer wavelength. Thus, under normal transmitted light pure chlorophyllic solution of chlorophyll-*a* appears as blue-green but when viewed in reflected light it gives a blood-red fluorescence. Similarly chlorophyll-*b* appears brownish-red in reflected light.

One of the striking properties of chlorophylls is that they can absorb certain wavelengths of light. Thus, when the chlorophyll solution is kept between ordinary light and a spectrometer¹, it is

¹ Instrument for producing and making measurements of optical spectrum.

found that certain wavelengths of light are absorbed more than others. Dark bands are seen in the spectrum when there is a complete absorption. Maximum absorption of both chlorophyll-*a* and chlorophyll-*b* takes place in the region of blue-violet, with peaks at about 429 $m\mu$ and 453 $m\mu$ respectively and the next maximum is in the red region of about 642 $m\mu$ and 660 $m\mu$ respectively (Fig. 8.3). Chlorophyll-*a* shows three distinct forms of bands on the basis of their maximum absorption in the red. They are chlorophyll-*a* 670, 683 and 695. The last two together with energy sink P_{700} are the only photosynthetically active pigment.

Although both chlorophyll-*a* and-*b* show apparently identical properties regarding solubility and absorption spectrum, but they have got differences in the degree of solubility (for example, ether is a good solvent for chlorophyll-*a*, while methyl alcohol is considered best for chlorophyll-*b*) and absorption spectrum (specific absorption of chlorophyll-*b* is more in the blue-violet region than chlorophyll-*a* and reverse in the far-red region).

Chlorophylls are neutral substances, changing its composition by slight change of the *pH*. Thus, when the chlorophyll solutions are treated with dilute acids, a waxy olive green substance is produced known as *phaeophytin*. If, however, they are treated with alkalis chlorophylls are saponified, yielding a water soluble green compound—*chlorophyllins*.

Chlorophylls and very much comparable to haeme of human blood and the cytochrome. The structural formula of both these substances suggests that instead of Mg occupying the centre of the chlorophyll structure, Fe occupies the central place of the structure of the haeme and lack a phytol tail. Further the decomposed end products are also same in both these cases.

Factors affecting chlorophyll synthesis: The synthesis of chlorophylls is mainly a physiological process that occurs in the living cells of the plant body. Like all metabolic activities, the synthesis of chlorophylls in plants is the result of a series of biochemical changes within the cell. These synthetic activities, ultimately leading to the formation of chlorophylls, are governed by a number of factors. Absence of any one of these factors will inhibit the synthesis of chlorophylls in plants and will develop a characteristic mottled condition of the leaves, which is known as *chlorosis*. Chlorosis may also be a consequence of the absence of any one of the essential mineral elements.

The following are the most important factors in chlorophyll synthesis.

(i) *Genetic factor*—The most essential condition for the formation of chlorophyll is the genetic factor. The cell can not synthesize chlorophyll when the genetic factor is lacking, even when all other factors are favourable. Since genes are the controlling centre of expression all the characteristic features of a plant, absence or

decrease of such a factor will, therefore, considerably inhibit or reduce its synthesis in plants. Thus the 'albino' condition of the seedlings is the ultimate expression of such a genetic abnormality in plants.

(ii) *Light*—It is another essential factor in the synthesis of chlorophyll, provided other factors are favourable. Although chlorophyll synthesis can take place in a very wide range of light intensity, still its presence is essential for the formation of chlorophylls. Light intensity helps in the conversion of leucoplasts to chloroplasts. Palladin (1922) is of opinion that the precursor of chlorophyll is *chlorophylligen* which can be produced even in the absence of light. But, for the further conversion of chlorophylligen to chlorophylls, light is essential. According to Eyster (1928), however, the precursor of chlorophylls is *prochlorophyll* ($C_{55}H_{70}O_4N_4Mg$) which in presence of light changes to chlorophyll.

The intensity of light for the synthesis of chlorophyll varies considerably, but low light intensity is found to be more effective than strong light. Strong light usually destroys the chlorophylls and consequently decreases the rate of chlorophyll synthesis instead of enhancing it.

Chlorophyll synthesis takes place in all wavelengths of visible spectrum provided it has got the adequate energy value. Light of the lower wavelength (440 $m\mu$) is more effective in inducing chlorophyll synthesis than lights of higher wavelengths.

(iii) *Oxygen*—Since two of the much complicated steps of chlorophyll biosynthesis involve the process of oxidation, oxygen therefore, plays an important role in the synthesis of chlorophyll. The stages where oxygen act, is in the formation of protoporphyrin and Mg-vinyl phaeoporphyrin from coproporphyrinogen and Mg-protoporphyrin respectively. In the absence of oxygen, therefore, no synthesis of chlorophyll can take place within the plant.

(iv) *Magnesium*—It is another essential element for the synthesis of chlorophyll, because the element directly enters into the composition of the chlorophyll molecule. Absence of magnesium, therefore, produces the characteristic mottled chlorosis in the leaves.

(v) *Iron, manganese, copper etc.*—These elements though do not enter into the chemical composition of the chlorophyll molecule, but are in some way essential for its synthesis and the absence of any one of these elements causes the characteristic chlorosis in the plants. The most important role of iron in chlorophyll synthesis is that it helps in placing the magnesium within the centre of the chlorophyll molecule. The role of other elements like manganese, copper, zinc etc. is also equally important as they are the constituents of the enzymes (oxidising-reducing, carboxylase etc.) many of which are actively involved in the reaction chains of chlorophyll synthesis.

(vi) *Carbohydrate*—Adequate supply of carbohydrate is necessary at the seat of chlorophyll synthesis. Since the initial reaction of

chlorophyll synthesis starts from glycine and succinic acid—the intermediate products of Krebs cycle, continuous supply of carbohydrates is necessary for chlorophyll synthesis.

(vii) *Nitrogen compound*—From the early inception of chlorophyll synthesis from glycine which is an amino acid and consequently contains— NH_2 groups upto the structure of chlorophyll, nitrogen and nitrogenous compounds are directly reacting in the system ultimately entering into the chemical composition of chlorophyll. Without nitrogen, many of the biosynthetic steps could not have taken place at all. Its importance in chlorophyll synthesis is therefore universally accepted.

(viii) *Temperature*—The maximum temperature at which chlorophyll synthesis proceeds in its rapidity varies considerably among species. The optimum temperature is, however, found to be between 26°C – 30°C (Lubimenko and Hubbenet, 1932). In some cases the optimum temperature, however, lies between 11°C – 20°C (Larsen, 1950).

8.2 Carotenoids: Associated with chlorophylls, the chloroplasts contain another group of fat-soluble pigments. These are orange β -carotene and yellow xanthophyll, together known as **carotenoids**. These substances are present in small amount in almost all higher plants and in many micro-organisms (red and green algae, photosynthetic bacteria etc.). Carotenoids like chlorophylls are located in the chloroplasts and in chromatophore. Both these pigments are sometimes attached to the same protein forming a complex known as *photosynthin* (Goodwin, 1960). Carotenoids are often called *lipochromes* as the pigments are soluble in fat and are closely associated with fatty substances.

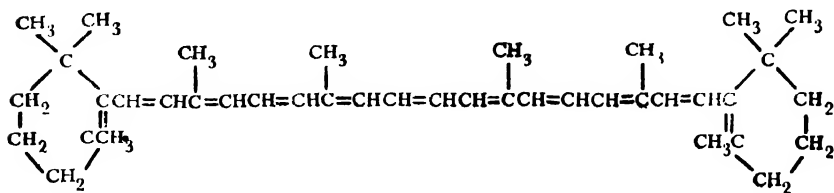


Fig. 8.4 Structure of β carotene. Note the symmetry and two ionone rings at the two ends.

Carotene is the most common carotenoid found in plants. It possesses an orange-yellow colouration. The name “carotene” was first given in 1831 by Mackenroder to a substance isolated from carrots. The structure of the carotene was definitely established only after 1925 from the work of Karrer, Kühn, Lederer. Carotene is the derivative of the red pigment—*lycopene*, found in tomato and other fruits and flowers. It is a highly unsaturated straight chain hydrocarbon having the formula $\text{C}_{40}\text{H}_{56}$.

Four important naturally occurring carotenes with the same chemical composition ($C_{40}H_{56}$) are named α -carotene, β -carotene, γ -carotene and δ -carotene of which β -carotene is only symmetrical and other three carotenes are asymmetrical. In all types of carotene, there are *ionone* rings either at one or both ends of the molecule. α - and β -carotene contain two ionone rings and γ - and δ -carotene have only such ring. The most characteristic feature of these carotene is the presence of a ring at one or both hydrocarbon chains (Fig. 8.4).

Like chlorophylls, carotenes are insoluble in water but readily soluble in alcohol, chloroform, benzene etc. They show the property of fluorescence—orange-red by transmitted light and green-blue by reflected light. Being unsaturated they are quickly oxidised in air changing till original colour takes place in scraped carrot. Another property of β -carotene is that it can absorb the blue-violet portion of the visible spectrum. β -carotene can be converted to vitamin A_1 *in vivo* and so it is termed as *provitamin A₁*.

The oxygenated carotenoid compounds are known as **xanthophylls**. These are yellow or brown pigments having the formula $C_{40}H_{56}O_2$. The most important xanthophyll is *lutein* obtained from the green leaves, flowers and fruits of sunflower. Lutein is an oxygenated derivative of α -carotene. Other xanthophylls are *lycoxanthin* obtained from tomato, *zeaxanthin* obtained from yellow corn, *cryptoxanthin* from green leaves and yellow corn, *cryptoxanthin* from green leaves and yellow corn, *violaxanthin* from green algae and *fucoxanthin* from brown algae.

TABLE 4

Major xanthophyll pigments of green leaves (From Goodwin, 1960)

Pigment	Structure
Lutein	3, 3-Dihydroxy α -carotene
Cryptoxanthin	3-Hydroxy β -carotene
Zeaxanthin	3, 3-Dihydroxy β -carotene
Violaxanthin	5, 6, 5', 6'-Diepoxyzeaxanthin
Neoxanthin	$C_{40}H_{56}O_4$ (?)

A few naturally occurring carotenoids contain carboxyl group which are found to be a derivative of other carotenoids due to oxidative cleavage. The important example is *bixin* ($C_{25}H_{20}O_4$) obtained from the pods of *Bixa orellana*, *crocin* ($C_{20}H_{24}O_4$) obtained from *Crocus sativus* (saffron) etc.

Biosynthesis of carotenoids—Although the biosynthetic process in the formation of carotenoids has been known considerably, very little is known about the metabolic interrelations among the various groups of carotenoids. It has been suggested that the C_{40} -compound which is formed first, is a colourless highly saturated *phytoene* (e.g. tetrahydrophytoene) which by subsequent dehydrogenation gives

rise to coloured carotenoids (e.g. lycopene) (Bonner, 1946 ; Griffiths and Stanier, 1956). According to Mackinney (1956), however, the biosynthesis of carotenoids does not agree with this hypothesis and according to him colourless phytoene and coloured carotenoids are synthesized by separate pathways from a common precursor and each C_{40} -compound is formed independently.

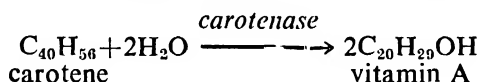
The biosynthesis of β -carotene (Grob and Butler, 1956) involves the initial conversion of C_2 units from acetic acid (probably acetyl co-A) to mevalonic acid followed by the formation of large isoprenoid compound.

Light is not essential in the formation of carotenoids. They are usually formed in darkness.

Physiological role of carotenoids—In majority of the green plants carotenoids occur together with chlorophylls in the chloroplasts and the phytol residue of the chlorophylls is found to have derived from the carotenoids—as both are related chemically. The possible role of carotenoids in photosynthesis is that by absorption of light the carotenoids may contribute energy to the photosynthetic process.

But this, however, must be secondary as tissues rich in carotenoids and devoid of chlorophylls do not photosynthesize. Duysens (1956) and others, however, believe that the energy absorbed by carotenoids is transferred to chlorophyll-*a* and used in photosynthesis.

In some of the plants the biochemical role of carotenoids is very much related with activity of vitamin A. β -carotene which is "provitamin A" splits in the middle. The product is the aldehyde corresponding to retinene which is then reduced to vitamin A.



Carotenoids participate in the phototropic responses of higher plants, fungi and bacteria (van Niel *et al*, 1950).

The action spectrum for phototropic bending in *Avena* seedling has two bands in the blue regions ($440m\mu$ and $470m\mu$) and it is these regions that carotenoids absorb most light. Since the *photo inactivation* of auxins on the illuminated side is mainly responsible for phototropic curvature, the carotenoids may activate the inactivation of auxins. Glaston (1950), however, suggested that it is the riboflavin and not the β -carotene which is active in auxin inactivation.

That carotenoids also protect against *photo oxidation* has been shown by Stanier (1959).

8.3 Anthocyanins and related compounds:—In green plants chlorophyll is localised in the grana of the chloroplast, carotenoids also remain within it. There is another group of pigments which are usually red, blue or purple in colour and found primarily in the vacuolar sap of the plant cell and are known as anthocyanins. They

are freely soluble in water and are important *water soluble pigments* in plants. This pigment is very common in the flowers, fruits and developing leaves. Anthocyanins are present in all members of the flowering plants with the exception of one order of higher plants, the Centrospermae. The red colour in plants of this order is due to *betacyanins*. Betanidin is the aglycone of *betanin*, the betacyanin of beet root. The red colour of the bracts of *Bougainvillea* is due to betacyanin. Originally it was thought that these pigments were related to anthocyanins, even though they contained nitrogen, they are in fact similar to the plant growth substances, the auxins, having the same basic indole ring structure. The related yellow pigments are known as *betaxanthins*. Colour of the anthocyanins depends on the pH of the medium. Generally in acid medium all the anthocyanins are red ; violet or purple at neutral pH values ; but the change in the blue colour results owing to further increase of pH of the medium (alkaline medium). Actually the acidity factor in the colour expression of anthocyanins has been to some extent over emphasised. Although it is true that a wide variation of colours can be obtained by changing the pH of the medium, but in nature it does not follow the same principle. Thus the *cyanin* of rose petals is red in pH 3, but the cyanin of corn flower is blue in the acid medium. Generally the cell sap concentration does not exceed 7, yet we observe a variety of blue or violet colouration of the flowers. So most of the blue or violet colouration of flowers is definitely not due to alkalinity of the medium. Thus, it has been found that the anthocyanin colouration of the flowers and fruits is due to accumulation of aluminium in the cell sap. Thus the blue colour of *Hydrangea*, a temperate plant, is due to an acid-stable delphinidin-aluminium complex. This metal complex of the pigment is therefore responsible for the blue colouration of the flowers and fruits even the cell sap is acidic. The blue colour of the corn flower is due to a colloidal substance which stabilise the blue colour in acid cell sap.

The colour patterns of spotted, striped and variegated flower petals are much more complicated than the natural colour patterns of anthocyanins. Anthocyanins are optically active and can absorb light within the range of 200-600 m μ and the maximum absorption is in the visible range.

Most of our knowledge regarding the chemistry of anthocyanins rests on the work of Willstätter and Robinson. Anthocyanins are glycosides with 1 or 2 carbohydrate units and the complex compound known as *anthocyanidin*. Anthocyanidins are the derivatives of 3, 5, 7-trihydroxy-flavylium hydroxide or 2-phenyl 3, 5, 7-trihydroxy-benzopyrylium hydroxide. There are three main groups of anthocyanidins (e.g. *pelargonidin*, *cyanidin*, *delphinidin*) with the number of hydroxyl group varying from 4 to 6 and any number of these hydroxyls may be methylated. The carbohydrate component in the glycosides are generally glucose, galactose or rhamnose and one or two carbohydrate units may be linked with the anthocyanidins.

Besides the above monosaccharides, anthocyanin may also contain a disaccharide e.g. gentiobiose and rutinose. It may even be a trisaccharide e.g. gentianose. Usually only one sugar molecule is present in a glycoside, but in cyanin (the red pigment of rose, dahlia, cornflower etc.) two sugar molecules are attached to the anthocyanidin. The sugar molecule is usually attached to 3-hydroxyl group of anthocyanidin. If more than one sugar is present, the second molecule is either linked with the first as in cyanin or it may be attached to the 5-hydroxyl group as in diglycosides.

The colour of the anthocyanins depends of the number of the hydroxyl groups and also on the extent to which the hydroxyl groups are replaced by methoxyl group.

Synthesis of anthocyanins is greatly influenced by genes and the sugar content of the tissues. Environmental factors like light intensity, low temperature, drought, low oxygen supply influence the synthesis of anthocyanin in plants. Anthocyanin synthesis can effectively take place in the ultraviolet rays. All the visible light of the spectrum can also be effective in their synthesis. In some cases (e.g. in the etiolated seedlings and in the roots of beet) formation of anthocyanin also takes place in absence of light.

Role of anthocyanins—The exact function of the anthocyanins is not known clearly but their bright coloured appearance certainly help them in cross pollination by attracting insects. They have been credited with protecting the chlorophyll from decomposition in strong light. They have some favourable influence on some of the enzymatic reactions in plants and consequently favouring indirectly the process of respiration and photosynthesis. They can absorb considerable amount of light and convert it into heat energy.

Another group of widely distributed water soluble plant pigments is the derivative of 2-phenyl 1, 4-benzopyrone commonly known as **flavone**. It is structurally related to the anthocyanins. It has been isolated from a number of plants including primrose. It is colourless but its hydroxylated derivatives e.g. flavones, flavonols and flavanones are yellow in colour. Like anthocyanins they usually contain hydroxyl group and the pigment occurs both in the free form and as glycosides.

The other groups of water soluble yellow pigments are the **chalcone** and the **aurones** named after their derivation from benzalacetophenone of chalcone and benzalcoumaran or aurone. These pigments also occur in the free state or as glycosides.

All the last three named pigments are normally colourless but when extracted and treated in various ways (including ammonia vapour) exhibit their typical yellow colouration. These groups of pigments are termed **anthoxanthins**.

List of some water soluble pigments

1. Anthocyanidins	{	Pelargonidin	3. Flavanones	{	Naringenin
		Cyanidin			Eriodictyol
2. Flavones and flavonols	{	Delphinidin	4. Chalcones	{	Liquiritigenin
		Peonidin			Dahlia chalcone
		Malvidin			Butein
					Okanin
	{	Chrysin	5. Aurones	{	Aureusidin
		Apigenin			Sulfuretin
		Luteolin			Maritimetin
		Kaempferol			
		Quercetin			

8.4 Biloproteins (Phycobilins): These are the main group of accessory plant pigments found only in certain algae. These red and blue pigments, *phycoerythrins* and *phycocyanins* which collectively called previously as *phycobilins*. The name 'phycobilins' was first proposed by Lemberg (1928) as this pigment has got a chemical affinity with the bile pigments of the animals. But O'heocha (1962) observed that the free pigment cannot be separated from a protein moiety and the name of the pigments was therefore changed from phycobilins to biloproteins to indicate the existence of the pigment-protein complex.

Biloproteins are present in only 3 algal divisions—the Cyanophyta, Rhodophyta and Cryptophyta. The species of Cryptophyta—*Cryptomonas*, *Rhodomonas* etc. however contain some unknown phycocyanin and phycoerythrin. These are the main photosynthetic pigments of these algal groups. These pigments are associated with the protein, so the study of these pigments comes from the studies of the pigment-protein complex. Their presence in higher plants is

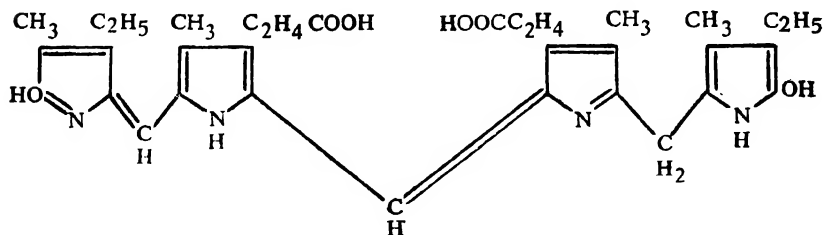


Fig. 8.5 The structure of the prosthetic group of phycocyanin. Phycoerythrin is similar in general structure, but here the prosthetic groups are attached to proteins.

still uncertain. Biloproteins differ from the other important plant pigments like chlorophylls and carotenoids in that these are water soluble, further these are associated with the plastids of red algae and with the cytoplasmic lamellae of the blue-green algae. In higher plants chlorophylls and carotenoids may be associated with protein

in the grana of the plastids like biloproteins, but their connection is very unstable. Whereas in biloproteins this protein-pigment association is very stable.

Regarding the chemical structures of these compounds, it has been found that these consist of an open chain tetrapyrrole. They are the compounds of carbon, hydrogen, oxygen and nitrogen and with no metal or phytol in their chemical structures. The chemical formula of phycocyanin is $C_{34}H_{44}O_8N_4$. Phycoerythrin, however, contains two extra hydrogen and the formula is $C_{34}H_{46}O_8N_4$. The molecular weights of these pigments are 273,000 and 290,000 respectively. Although different forms of phycoerythrins and phycocyanins have been isolated from different plants, they are basically same; only difference is in their nature of protein components rather the pigments itself. As for example, the forms R-phycoerythrin and C-phycoerythrin differ on the plant source and consequently on the nature of protein part. The former has been isolated from red alga, whereas the latter from blue-green algae. Similar is the case of R-phycocyanin and C-phycocyanin. When they are isolated both from red and blue-green algae they are known as P-phycocyanin and P-phycoerythrin respectively.

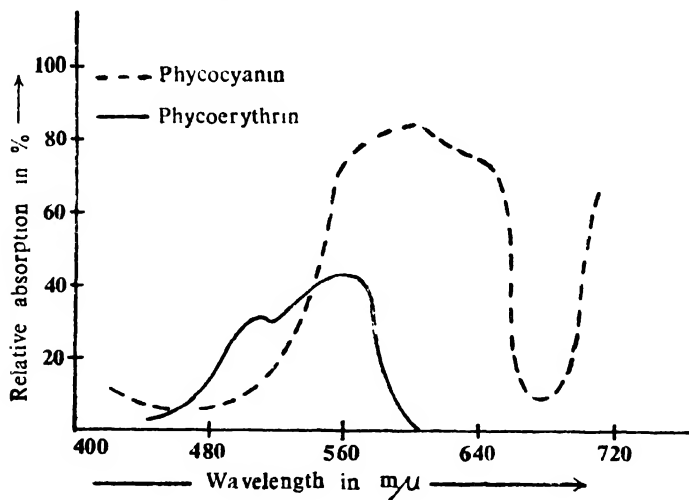


Fig. 8.6 Absorption spectra of phycocyanin and phycoerythrin.

Absorption spectra of biloproteins clearly indicate that these pigments are active in the transfer of light energy to chlorophyll for their utilization in photosynthesis. R-phycoerythrin (mainly obtained from red algae) has three absorption zones at 495, 540 and 565 $m\mu$ and the maximum absorption being in the green region (Fig. 8.6). C-phycoerythrin (mainly obtained from blue-green algae) has got a maximum absorption in the green region (550 $m\mu$). Another phycoerythrin, P-phycoerythrin has got an absorption spectra at

green (550 $m\mu$) and yellow (565 $m\mu$) regions. For R- and C-phycoerythrin the maximum absorption peak is at orange (615 $m\mu$), a small absorption band has, however, been found in the green (550 $m\mu$) in case of R-phycoerythrin. In case of P-phycoerythrin the absorption peaks move further to orange (650 $m\mu$).

Like carotenoids, the role of biloproteins in photosynthesis is indirect. The energy absorbed by these pigments transmit their energy to chlorophyll, when they become 'active' in photosynthesis. The photosynthetic efficiency of these pigments is far greater than chlorophyll-*a*. The role of chlorophyll-*a* in blue-green and red algae is minor and subsidiary. Major light absorption takes place through these biloproteins.

TABLE 5
Pigments in plants and photosynthetic bacteria.

Group of Plants	Chlorophylls	Carotenoids	Other Pigments
Green plants	<i>a</i> and <i>b</i>	β -Carotene and lutein	Anthocyanins (non-photosynthetic)
Green sulphur bacteria	Bacterioviridin	Several	—
Purple sulphur bacteria	Bacteriochlorophyll	Spirilloxanthin	—
Diatoms	<i>a</i> and <i>c</i>	Fucoxanthin	—
Brown algae	<i>a</i> and <i>c</i>	Fucoxanthin	—
Yellow-green algae	<i>a</i> and <i>e</i>	Several	—
Red algae	<i>a</i> and <i>d</i>	β -Carotene and lutein	Biloproteins (phycoerythrin and phycoerythrin)
Blue-green algae	<i>a</i>	Several	Biloproteins

8.5 Experiments on plant pigments :

A. PLASTIDAL PIGMENT :

(i) *Extraction of the chloroplast pigments*—Take about 50 g of leaves and spread them in an oven at 50°C and allow them to dry. Grind them in a Waring blender or simply chop them into small pieces.

Place the leaf powder or chopped leaves in a small conical flask containing 95% ethyl alcohol (or 80% acetone) and a pinch of CaCO_3 . After a considerable period the alcohol (or acetone) will dissolve out the chlorophyll and a deep green solution results. Filter the solution on a Buchner flask. The filtrate is an alcohol or acetone extract of chlorophyll-*a*, chlorophyll-*b*, carotene and xanthophyll as well as other alcohol or acetone soluble compounds in the leaf tissue.

(ii) *Separation of the green and yellow pigments*—Shake gently about 20 ml of the acetone extract [obtained in experiment (i)] with 40 ml of the ether in a separating funnel. Then pour 60 ml of distilled water down the side of the separating funnel. The mixture separates into two layers. Now draw off the lower acetone-water layer and discard by opening the stop cock of the separating funnel. The pigments are all now in the ether layer. Wash this solution again with water, draw off and discard the lower layer again.

Take about 10 ml of this ether solution of pigments in a small flask and add 5 ml of 30% methyl alcoholic potassium hydroxide solution and shake. Allow it to stand, when first the disappearance of the green colour and shortly after its reappearance will be observed. Add now 20 ml of distilled water and 5 ml of more of ether. On shaking the flask the two layers will be separated out of which the lower aqueous alkaline layer contains green pigments and the upper ethereal layer contains yellow carotenoid pigments.

(iii) Complete separation of four chloroplast pigments :

(a) *Separation of chlorophyll-a and-b*—In a separating funnel add 15 ml of petroleum ether and 10 ml of acetone extract of leaf pigments (obtained in expt (i)). Shake these two liquids gently by rotating the separating funnel. And now excess of distilled water (about 20 ml) gently down the side of the funnel and shake it again. Two layers are formed of which the upper layer is deep green. Draw off and discard the lower acetone-water layer. Repeat this washing with water again and discard the lower layer.

Now add 10 ml of 92% methyl alcohol in this petroleum ether solution. Shake the funnel and allow it to stand after which two layers will be observed. The upper petroleum ether layer contains chlorophyll-a (together with carotene) and the lower methyl alcohol layer contains chlorophyll-b (together with xanthophylls).

Draw off the two layers into two separate flasks and save them for further work.

(b) *Separation of two yellow pigments—carotene and xanthophyll*—Take 10 ml of methyl alcohol soln. in a separating funnel and to it add 10 ml of ethyl ether. Shake the mixture and pour small portion of distilled water (about 5 ml) down the side of the funnel, two layers will be observed of which discard lower methyl-alcohol layer. The pigments should be in the upper ether layer. Repeat the process for about 5 times to wash off the mixtures and similarly discard the lower methyl alcohol layer.

Now take two 25 ml flasks. To one add 10 ml of petroleum ether solution [obtained from expt. iii (a)] and to other add 10 ml of ether soln. About 5 ml of freshly prepared 30% methyl alcoholic potassium hydroxide soln. pour down the walls of each flask. Then add about 10 ml of distilled water; shake each flask and allow them to form two layers.

Of the two layers in the petroleum ether flask upper petroleum ether solution contains chlorophyll-a and the lower methyl alcoholic layer contains carotene. In the other flask, the upper ethereal layer contains xanthophyll and the lower aqueous alkaline layer contains chlorophyll-b.

(iv) *Separation of leaf pigments by filter paper chromatography*—Take some fresh leaves in a small beaker. Add sufficient boiling water to immerse the leaves. Clean all dirt from the leaves and decant off the water. Now grind the material thoroughly with about 1 g quartz sand and 10-15 ml. of 50 : 1 petroleum ether : methyl alcohol solution. Decant approximately 1 ml of the pigment extract into a test tube.

Cut a strip of filter paper with its width slightly less than the inside diameter of the large test tube and its length should be such that it can hang freely as shown in Fig. 8.7. Cut notches in one end of the strip paper. Now pierce a paper clip into both the sides of the cork.

Now using a fine pointed pipette place a drop of the above extract between the notches and allow it to dry again. Four such drops of extract were added on the same point and dried. Pour some solvent (8% acetone, 92% petroleum ether) into the test tube so that the level of the solvent lies behind the notches of the filter paper (below the spot). Hang the paper through the chip of the cork and place the tube in an upright position. When the upper edge of the solvent reaches

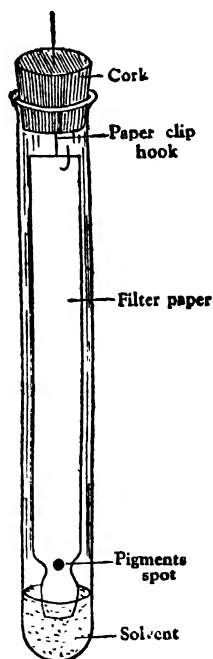


Fig. 8.7 Apparatus to show the simplest kind of chromatography to separate some of the plant pigments.

near the clip, remove the cork and hold the filter paper until the solvent has dried. It will be observed that the yellow zones (chiefly carotene) go well in advance of the green zone and the other pigments (chlorophyll -a, -b and xanthophylls) are absorbed near the point of contact where the upper bluish green zone (chlorophyll -a) and the lower yellowish green zone (chlorophyll -b) can be distinguishable. Xanthophyll can be 'visible' as yellow band above the bluish-green zone of chlorophyll -a.

(v) *Experiments on properties of chlorophylls :*

(a) *Solubility test*—That chlorophylls are insoluble in water and soluble in a number of organic solvents can be demonstrated by the following experiment.

1 g of oven dried suitable leaf powder was weighed and each sample was then placed in separate test tube with 10 ml of the following separate solvents to each : 95% methyl alcohol, acetone, benzene, petrol ether, 95% ethyl alcohol, chloroform and distilled water. Compare the degree of solubility (by visual colouration in each solvent) and it can be inferred that chlorophylls are soluble (although degree of solubility varies and the best being in 90% acetone and alcohol) in almost all the above solvents but not in distilled water.

(b) *Property of fluorescence*—Another important optical property of chlorophylls is that they can exhibit the property of fluorescence and can be demonstrated by the following way.

Take a test tube and fill it up partly with the chlorophyll solution. It is then kept for few hours in reflected light. After few hours it becomes blood red indicating its property of fluorescence.

(c) *Chlorophylls contain more than one pigments*—That chlorophylls contain more than one pigments can be exhibited by the method shown in experiments (ii) and (iii).

(d) *Absorption band of chlorophylls*—Prepare some green raw chlorophyll extract from suitable plant leaves [refer experiment (i)]. When a portion of such raw extract in a test tube is placed between a spectroscope and source of light, a black dark band is observed in the red and in the blue-violet region of the spectrum indicating that chlorophylls can absorb wavelength ($\pm 400 m\mu$ and $\pm 600 m\mu$) of visible light.

(e) *Replacement of Mg by Cu, Zn or Fe*—To an alcoholic extract of chlorophylls from suitable leaves [refer experiment (i)], when conc. HCl was added drop by drop, the green colour changes to brownish green chlorophyll molecule. This compound is known as *phaeophytin*. When such a compound was examined against a spectroscope, it shows a new absorption line indicating that the compound is not a chlorophyll.

To a portion of such compound when a crystal of copper sulphate, zinc sulphate or iron acetate are added and is heated gently, the colour of the solution changes back to its original deep green colour as the Mg of the chlorophyll molecule has been replaced by Cu, Zn or Fe.

(vi) *Effect of light on chlorophylls*—Take three test tubes and mark them as A, B and C. Place about 20 ml of crude chlorophyll extract to each of the test tube and keep one tube each in the dark (A), diffused light (B) and direct sunlight (C). After about one hour note the change of colour of the pigments. The colour of the first tube marked A remains unchanged while that of C changes its colour to yellowish-brown, B exhibit an intermediate colouration.

(vii) *Role of light in the formation of chlorophylls*—Plant some corn grains in a small pot and keep it in dark cabinet. Allow other conditions suitable for germination. The seedling exhibit a pale colouration of the leaves which, however, change their colour to green when kept in the light.

B. CELL-SAP PIGMENTS :

(i) *Extraction and properties of anthocyanin pigment*—Take approximately 20 g of red beet or red cabbage tissue and immerse them in a conical flask.

Add about 100 ml of distilled water and then heat the water to boiling (upto 80°C). The solution was then filtered and 5 ml of extract was taken in a test tube. To a solution in one tube few drops of 0.1N NH_4OH were added and shaken and compared its colour with the untreated solution of the test tubes. The solution turns distinctly blue. To this solution add few drops of 0.1N acetic acid, drop by drop, the blue colour again changes to its original colour and on further addition of acetic acid it changes to red colour.

It shows that the anthocyanins are very much sensitive to pH of the medium. is blue in alkaline medium and red in acidic medium.

SELECTED QUESTIONS

1. What are chlorophylls ? Describe the chemistry and synthesis of chlorophylls.

Refer topics *chemistry of chlorophyll* and *biosynthesis of chlorophyll* in article 8.1

2. What is the chemical composition of chlorophylls ? Discuss the factors influencing chlorophyll synthesis.

Refer *chemistry of chlorophylls* and *factors affecting chlorophyll synthesis* in article 8.1

3. Describe the properties of chlorophylls and compare it with other plant pigments.

Refer the topic *properties of chlorophylls* in article 8.1 and introduction part of articles 8.2, 8.3 and 8.4

4. What are water soluble pigments in plants ? Give an account of them.

Refer articles 8.3 and 8.4

5. Mention the important plant pigments and state the biological significance and chemical nature.

Refer *introduction* of Chapter 8. For 'biological significance' refer *the role of chlorophylls, carotenoids and anthocyanins* in article 8.1, 8.2 and 8.3 respectively. For the chemical nature of chlorophylls refer question no. 1 and for carotenoids and anthocyanins refer *introduction* part of article 8.2 and 8.3 respectively.

6. Write a short essay on plant pigments with particular reference to their occurrence, chemistry and function.

Refer *introduction* of Chapter 8 ; refer topics *introduction* and *chemistry of chlorophylls* in article 8.1 ; refer topics *introduction* and *physiological role of carotenoids* in article 8.2 and refer article 8.3.

CHAPTER 9

Photosynthesis

9.1 Definition : *It is the process in which carbohydrates are synthesized in green cells exposed to light from carbon dioxide and water absorbed from air and soil respectively.*

Like all plants, green plants require considerable amount of (a) oxidizable organic food materials (b) mineral elements and (c) water. The green plants being autotrophic are able to reduce the carbon dioxide to the level of sugar with the help of radiant energy and the photosynthetic apparatus.

9.2 Early investigation : J. B. van Helmont (1577-1644), Flemish physician and chemist, was the first who tried to solve the mystery of plant nutrition in the earlier part of the 17th century. He also ruled out the idea of the earlier workers that soil was not the principal source of food of green plants. Although van Helmont's idea was a premature one, still the credit goes to him as it starts the enquiry into the life's chain which we call **photosynthesis**.

In 1727 Stephen Hales pointed out the importance of leaves and suggested that plants probably draw through their leaves some part of their nourishment from the air and light also by entering the leaves contribute much to the nutrition of plants. But towards the end of the 18th century air became a new centre of interest for scientists and Joseph Priestly (1772), English clergyman and chemist and his contemporaries demonstrated the biological importance of atmospheric oxygen in the process of photosynthesis. At about the

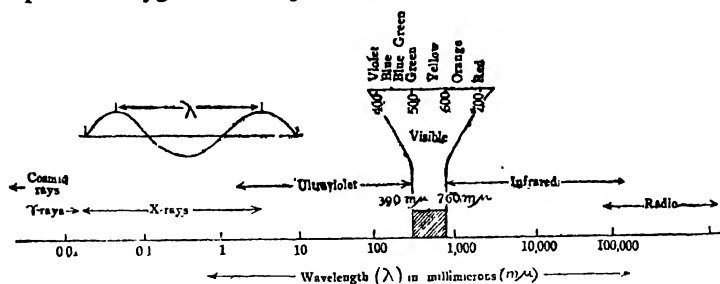


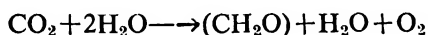
Fig. 9.1 The spectrum of radiant energy on a logarithmic wavelength scale. The green plant can utilize a portion of visible light in photosynthesis.

same time Jan Ingen-Housz (1779), Dutch physician and naturalist pointed out that sunlight was essential for the production of oxygen by green plants.

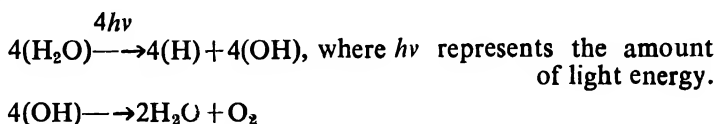
The link was further strengthened by Swiss naturalist Jean Senebier (1782) who discovered that plants absorb carbon dioxide from the atmosphere, although the exact relationship of carbon dioxide in photosynthesis could not be worked out at that time. Some twenty years later, de Saussure (1804), Swiss chemist and naturalist showed that both water and carbon dioxide were involved in the synthesis of organic substances by green plants in presence of light. Then in 1818 Pelletier and Caventou introduced the term '*chlorophyll*' for the green colour of the plants and in 1862 Sachs mainly centered round his idea on the chloroplasts which according to him is the main site of photosynthesis. Chloroplasts are also the centres of the oxygen evolution in photosynthesis came from the work of Engleman (1882).

Thus by the end of 19th century the three key factors of photosynthesis—carbon dioxide, light and water—have been investigated thoroughly and some of the pieces of the puzzles have not been solved until the middle of twentieth century particularly with the complete chemical study of the chlorophylls based on the classical work of Willstätter and Stoll (1913 ; '18). Then from the classical work of Blackman (1905) regarding the relationship of photosynthesis with light intensity, temperature and carbon dioxide, follows the work of Warburg, van Niel (1930, '31), Emerson and Arnon (1932) who came to the conclusion that in the process of photosynthesis there are two reactions—'light' and 'dark'.

According to van Niel (1930 ; '31) the equation for photosynthesis should be



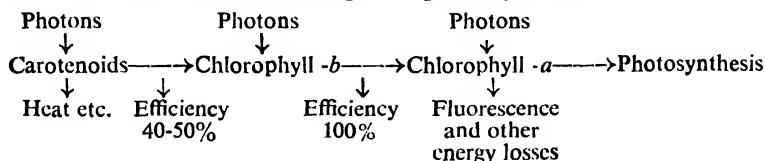
where two molecules of water must react to reduce carbon dioxide upto the level of carbohydrate, van Niel further suggested that the photo-decomposition of water yields [H] which is directly concerned with the reduction of carbon dioxide and [OH] whose decomposition yield oxygen according to the equation



This photochemical decomposition of water i.e., photolysis of water has been clearly demonstrated by Hill (1937) and Ruben (1941).

It has been experimentally proved that the conversion of six molecules of carbon dioxide to one molecule of glucose requires approximately 690 kgcals of energy. This energy is mainly obtained from the radiant energy of visible light (4000 to 7000 Å) absorbed by chlorophylls.

Light is emitted as certain particles called *photons*¹ which are absorbed by the pigments of the plants for photosynthesis. Chlorophylls are the main pigments which absorb light for photosynthesis. However, light may be absorbed by the carotenoids and other pigments and are also effective in photosynthesis. In any way light absorbed by carotenoids is transferred to chlorophylls which finally provides the energy for photosynthesis. Carotenoids transferred the light energy to chlorophyll -b and then to chlorophyll -a which finally provides the energy for photosynthesis



All these foregoing discoveries help up in understanding the basic steps of photosynthesis, no real understanding in the biochemical pathways came until 1950 when Calvin and his associates (1956) first came to a significant advance in the conversion of carbon dioxide and water to carbohydrate during photosynthesis with the help of radioactive isotope (¹⁴C).

Although the lacunae in understanding the process of photosynthesis have been solved recently but many more things yet to be discovered to correlate the process with the different environmental factors.

9.3 Locale of Photosynthesis: The simplest organelles of photosynthesis are found in the bacteria and blue-green algae. In these organisms, unit membranes (cytomembranes), are differentiated as independent *lamellae* or *vesicles*. Lamellae occur as double membrane structures formed by two unit membranes lying in close apposition. The cytomembrane of many photosynthetic bacteria are differentiated as independent vesicular structures known as *chromatophores*. These bodies which are surrounded by a membrane, measure about 150Å in diameter and are scattered through the cell cytoplasm.

Double membranes appear to represent the *basic structural units* of all photosynthetic organelles.

With the exception of blue-green algae, other algae and cells of higher plants carry out photosynthesis in ordered, membrane-bound structure called *chloroplasts*². The association of photosynthesis

¹ It is represented by $h\nu$ which means

$E \text{ (energy)} = h\nu$, where h = Planck's constant (6.65×10^{-27} ergs/sec), ν is the frequency of radiation = $\frac{c}{\lambda}$, where c = velocity of light (3×10^{10} cm/sec)

and λ = wavelength in cm.

² For detail structure refer Chapter 3 article 3.2

with specialised cytoplasmic structure (lamellae, chromatophores and chloroplasts) is the result of localization of the photoactive pigments especially *chlorophylls* in the membranes comprising the structural framework of these organelles. The pigment molecules are incorporated into the membranes in some ordered manner, possibly as a monolayer. The efficient capture and transfer of light energy probably results from the aggregation of pigments into groups of several hundred chlorophyll molecules and a smaller number of accessory pigment molecules (carotenoids, biloproteins). These

TABLE 6
Important Photosynthetic Pigments

Plant groups	Principal chlorophyll	Accessory chlorophyll	Other accessory pigments
Green plants	Chlorophyll -a 683 Chlorophyll -a 695	Chlorophyll -b 560, 480 Chlorophyll -a 670	Carotenoids (β -carotene and lutein)
Green algae	Same	Same	Same
Brown algae	Chlorophyll -a	Chlorophyll -c	β -carotene and fucoxanthin
Red algae	Chlorophyll -a	Chlorophyll -d	β -carotene : phycoerythrin and some phycocyanin
Blue-green algae	Chlorophyll -a		Several including phycocyanin and phycoerythrin
Diatoms (flagellates)	Chlorophyll -a	Chlorophyll -c	β -carotene and fucoxanthin
Purple bacteria (both sulphur and non-sulphur)	Bacterio chlorophyll		Different carotenoids (including lycopene, rhodospin, spirillo-xanthin)

aggregates of pigment molecules are considered to function as more or less independent *photosynthetic units*. These photosynthetic units are centered in some small particles in the membrane component of the granum disc. These particles called *quantosomes* (the word was first coined by Park *et al* in 1963) are the basic building blocks of the pigment containing membranes of the grana. The lamellar apparatus is made up of stacked subunits called *thylakoids*. These subunits correspond to a physiological unit of photosynthesis. The molecular weight of *photosynthetic unit* is about 2×10^6 and contain 230 chlorophyll molecules, 48 carotenoids, 46 quinones, 116 phospholipids, 500 galactosylglycerids, 48 sulpholipids, sterols and other lipids. Thus the molecular weight of total lipids is about 106 and that of proteins about 10⁶. The unit also contain cytochrome *b₆*, cytochrome *f*, 5 ferredoxin, 5 plastocyanin molecule and 2 manganous ions.

All the photosynthetic pigments of the cell are localised preponderantly in and around the lamellae. The latter on isolation and purification found to contain phospholipids and lipoproteins and

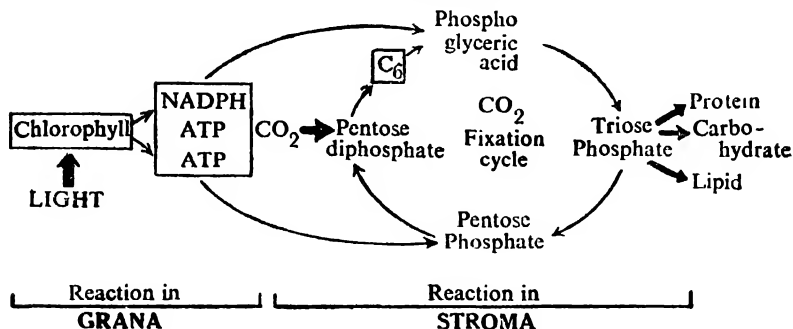
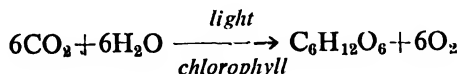


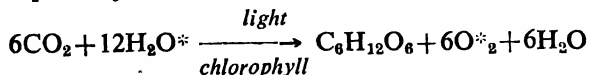
Fig 9.2 Location of two major reactions of photosynthesis in the chloroplasts is shown.

therefore are capable of catalyzing some of the most characteristic reactions of photosynthesis : the *photolysis of water* and reactions responsible for *electron transport*.

9.4 Mechanism of photosynthesis : In the 19th century and the early part of the 20th century a large number of scientists tried to find out the amount of carbon dioxide and water taken in by the green plants and the amount of energy-rich carbon compound and oxygen formed therefrom. For a long time the only recognizable products of photosynthesis have been considered to be simple sugars (such as glucose) and insoluble starch (which are the derivatives of glucose). For this reason the process of photosynthesis has been thought to be the reverse of respiration and the overall equation for the process is



The above equation although balanced is not entirely accurate as it will give an erroneous idea regarding the mechanism of photosynthesis. Since it has been found by labelling oxygen of CO_2 and H_2O^* (i.e., by using radioactive oxygen, ^{18}O) that all the oxygen liberated in the process comes from water and not from carbon dioxide (as has been previously believed). Twelve molecules of water must enter into the reaction to satisfy this requirement and the overall equation of photosynthesis should, therefore, be



The above equation indicates merely the beginning and the end of the process, but it does not tell us anything about the intermediate steps which follow a series of complicated stages before ultimate

conversion to sugar. Events in the process of photosynthesis occur so rapidly that it was practically impossible until recently to identify the intermediate substances involved in the process. In 1905 Blackman, however, succeeded in solving partly the process and suggested that the process would take place in two distinct sets of reactions. The first one is called the *light reaction* or *photochemical reaction* and occurs only when the green plant is exposed to light. This is immediately followed by dark reaction or *chemical reaction* where light is not necessary.

Within the 'light' phase there are two partial processes. First, is the absorption of light by chlorophyll to become 'excited' and the second phase is the transformation of excited energy to chemical energy. The first is purely a physical process completed within 10^{-11} to 10^{-9} seconds and the second is the photochemical process which lasts for 10^{-9} to 10^{-4} seconds.

The conversion of light energy to chemical energy (Light Reaction)—In the light reaction of photosynthesis, the light energy is absorbed and transformed into chemical energy which is temporarily stored with the cell in two compounds. These compounds are adenosine triphosphate (ATP) and reduced nicotinamide adenine dinucleotide phosphate¹ ($\text{NADPH} + \text{H}^+$) which are required in the reduction of carbon dioxide in photosynthesis.

To understand how light energy is transformed in photosynthesis it is necessary to discuss briefly about the effect of light on the electrons of chlorophyll. Electrons have the least energy when they are in their most stable state in a molecule. When an electron in the ground state absorbs light energy, it becomes 'excited' as a consequence of being raised to a higher energy level. This excitation generates an electron vacancy or *positively charged hole* (+) in the ground state that exerts a pull on the excited electron and favours its spontaneous return to the ground state. The chlorophyll molecule is well suited for capturing light energy and facilitating its transfer.

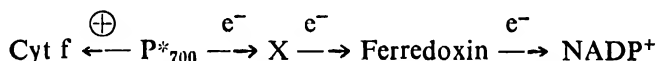
The first event in photosynthesis is the absorption of light by chlorophyll to produce the 'excited' state of this molecule. Interaction of the excited chlorophyll with water then occurs to separate an *oxidant* [O] and a *reductant* [R]. In the older literature the oxidant and reductant were regarded as products arising from the light dissociation (photolysis) of water and were designated as hydroxyl (OH^-) and hydrogen (H^+) ions respectively.

More recent schemes of photosynthesis show the oxidant and reductant not as products of water but as entities generated by the excited chlorophyll itself. In this view, the excitation of chlorophyll by light is considered to result in the *ejection* of an electron from the chlorophyll structure. This electron combining ultimately with NADP^+ to accomplish the reduction of this molecule—,

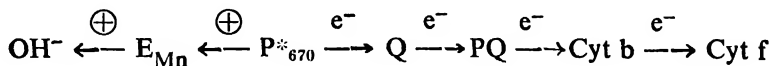
¹ Formerly known as triphospho pyridine nucleotide (TPN).

had to be excited for photosynthesis to occur. Among the possible arrangements of a system of 2 pigments, Hill and Bendall (1960) proposed a "series formulation" or "Z-scheme" very close to that currently accepted by most workers. In this scheme one pigment called P_{700} absorbs light at 700 $m\mu$ and another which we call P_{670} absorbs light at 670 $m\mu$. P_{700} and associated electron transport chain compose "System I" (PSI) and P_{670} and its electron transport chain compose "System II" (PSII) and the reducing end of the system II acts as a bridge between to two.

System I consists of some 300 molecules of non-fluorescent chlorophyll *a* with its main absorption in the far red. Associated with it one molecule of photo-oxidizable pigment P_{700} ($\lambda_{max} = 700-705 m\mu$) directly concerned with the primary photochemical reaction. In green plant this system also contains one molecule of cytochrome-*f* and perhaps less tightly coupled one unit of ferredoxin¹. The principal function of system I is the simultaneous generation of a strong reductant and of a weak oxidant. System I operating by itself, in the presence of an oxidizable donor DH_2 is responsible for photoreduction. The movement of electrons and 'holes' or positive charges for system I is,



System II is the "accessory pigment system". It contains approximately 100 molecules of chlorophyll *a* 670 - a fluorescent form of chlorophyll *a*, absorbing at shorter wavelength than the chlorophyll *a* of system I; it also contains chlorophyll *b* and other accessory pigments (ch-*c*, ch-*d* and ch-*e* as well as the phycobilin pigments depending on the organisms). System II is thought to consist of components with more positive (i.e. more oxidising) redox potential whose function is to oxidise OH^- to O_2 . This strong oxidizing system contains a manganese (Mn^{2+}) component (labelled here as $E_{Mn^{++}}$). The electron acceptor is called 'Q' for 'quencher'. The electron transport system following Q probably contains plastoquinone (PQ) which then reduces cytochrome. The electron and 'hole' transport system of system II is as follows:



A correlated function of system II is the formation of a weak reductant, perhaps reduced plasto or some other quinone, capable of regenerating Chl from Chl^+ produced by system I. System II operating by itself is responsible for the Hill reaction.

¹ Ferredoxin is an iron containing protein with an unusual structure.

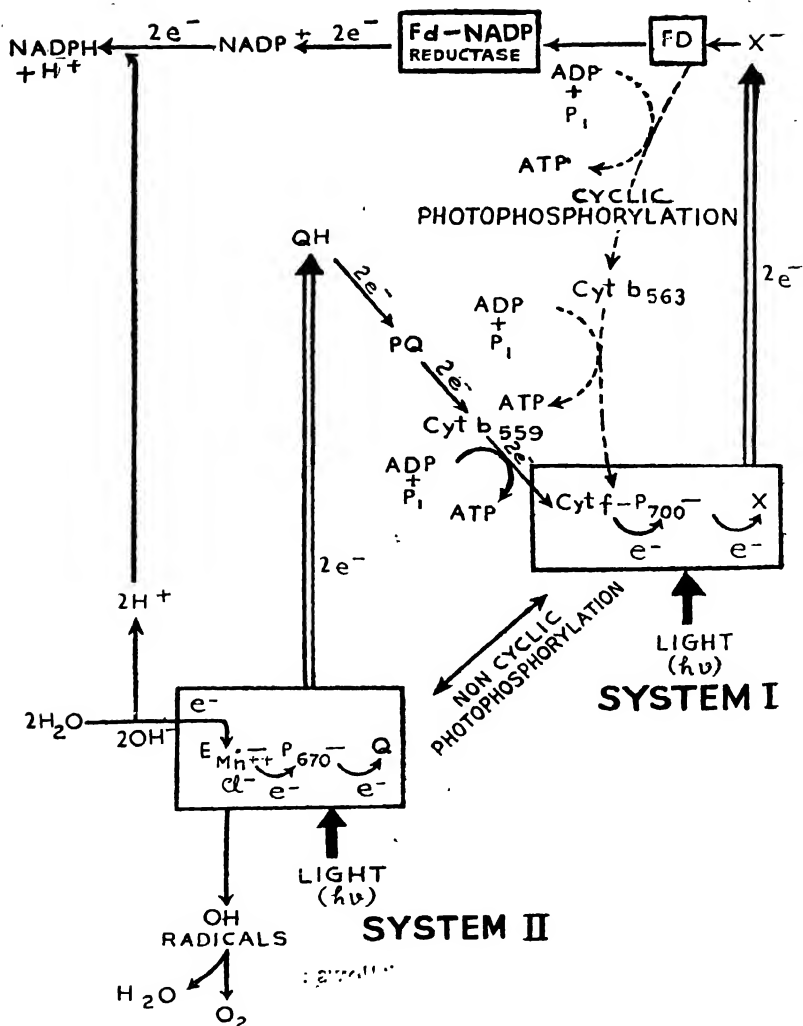
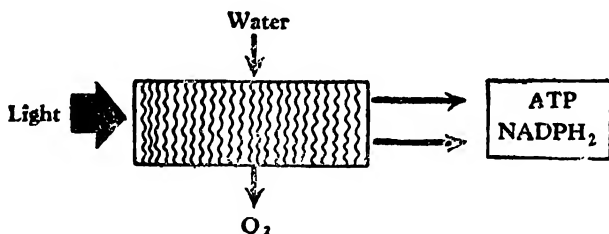


Fig. 9.4 Scheme for the series formulation (z-scheme) of photosynthesis. *System I* consisting of P₇₀₀, a long wavelength form of chlorophyll, is complexed with cyt f and electron acceptor X. When P₇₀₀ is excited, the electron path is P₇₀₀ → X → Ferredoxin (FD) → NADP⁺. P₇₀₀ receives an electron from cyt f. From ferredoxin the electron instead of reducing NADP⁺ can move through lower redox potential and enter Cyt f via Cyt b₅₆₃. This is known as *cyclic photophosphorylation* which involves only System I. Cyt f can also receive electrons from *System II*. System II consists of P₆₇₀, an enzyme complex (EMn⁺⁺) and an electron acceptor Q.

This system is operating in series and linked by an electron transport chain associated with *non-cyclic photophosphorylation* ultimately giving the electrons to Cyt f of System I. The positive charge reacting with OH⁻ to yield O₂.

Thus the light energy absorbed by photosynthetic system could lead to the esterification of inorganic phosphate into ATP was first demonstrated by Frenkel (1954) with bacterial chromatophore fragments. Arnon and his collaborators (1954) were able to carry the same reactions with chloroplasts and since then the occurrence of phosphorylation during electron transport in photosynthesis (or *photophosphorylation*) has been well demonstrated. The most important process that is linked to the tapping of biochemical energy in ATP is the one that—with the intervention of ETS (quinons, cytochromes etc)—links the reduction of the photochemically generated oxidant of system I to the oxidation of reductant generated by system II in green plants or the external reductant DH_2 in bacteria.

When the OH^- ions from water lose an electron it becomes an OH radical. 24 such OH radicals unite to form twelve molecules of water and six molecules of oxygen—it is this oxygen that is given off by the photosynthesizing organisms. The overall summary of the light reaction is given below.



Fixation of CO_2 and path of carbon in photosynthesis (Dark Reaction)—In the foregoing discussion the role of chlorophyll has been studied only in relation to its function in providing energy for the fixation of carbon dioxide and its subsequent reduction to multi-carbon molecules. These reactions can be carried out in complete darkness.

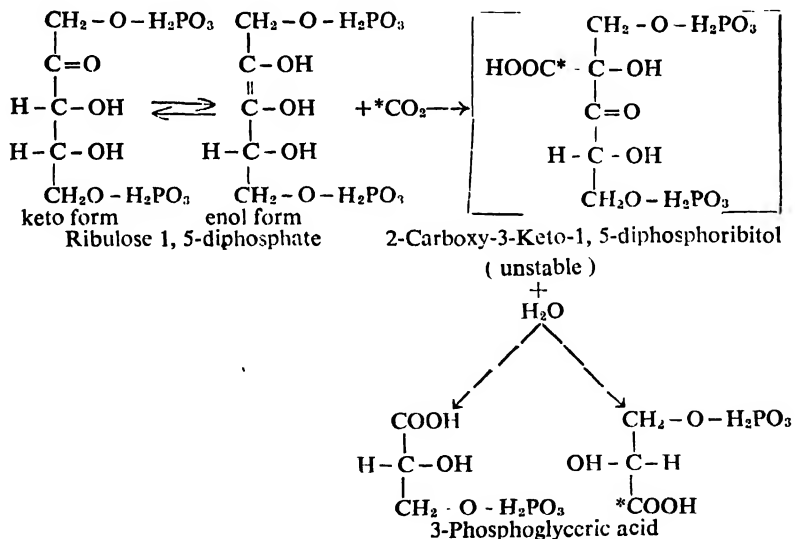
Significant advances in the elucidation of chemical reactions in the conversion of carbon dioxide and water to carbohydrate during photosynthesis have come from the work of Calvin and his associates (1956). They used the radioactive isotopes of carbon (^{14}C) and studied the radioactive substances formed from $^{14}\text{CO}_2$ by photosynthetic algae like *Chlorella* or *Scenedesmus*.

The stable compound formed in photosynthesis is found to be a 3-carbon compound known as phosphoglyceric acid (PGA). It has been found by Bassham and Calvin (1957) that the radioactive carbon is present in the carboxyl group PGA.

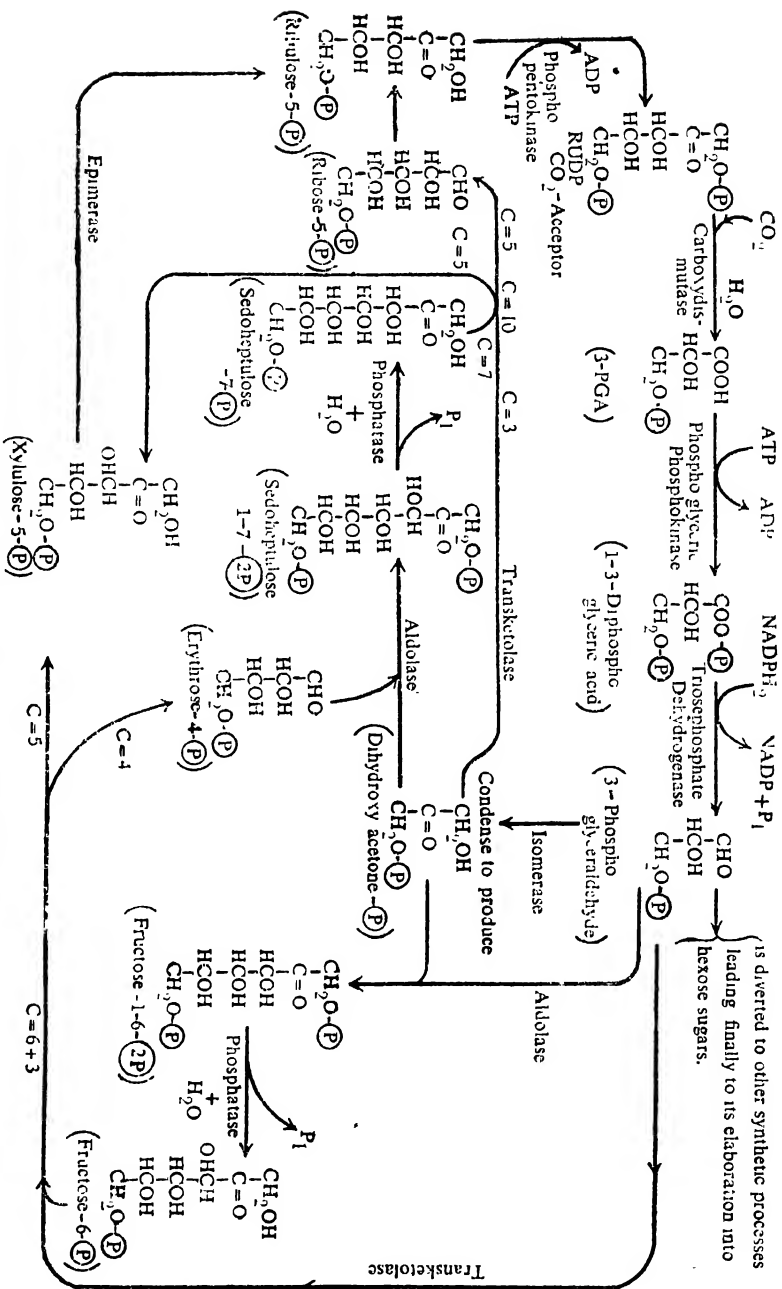
It has been found by Calvin (1962) that the fixation of carbon dioxide in photosynthesis proceeds according to a cycle—known as

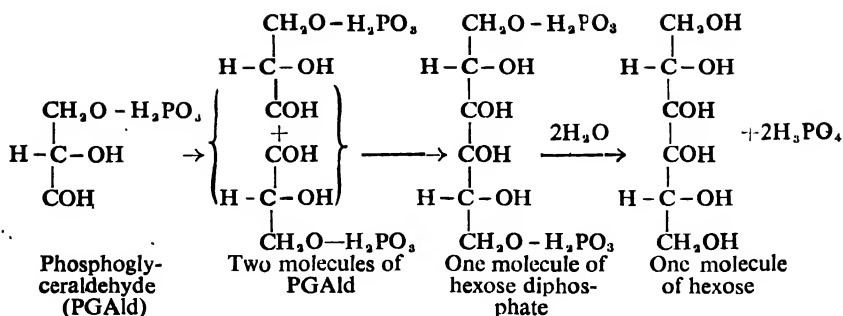
Calvin-Bassham cycle (Fig. 9.5). According to this cycle carbon dioxide combines with a 5-carbon sugar ribulose 1,5-diphosphate (abbreviated as RuDP) to give two molecules of PGA which are later on reduced to trioses. The whole process of carboxylation and subsequent reduction occurs three times for each turn of the cycle. So three molecules of RuDP and three molecules of carbon dioxide must combine to give six molecules of PGA. Five molecules of this 3-carbon sugar then by condensation and intramolecular transformation cause the formation of three molecules of RuDP. The cycle is thus complete with the regeneration of carbon dioxide acceptor (RuDP) and with the net gain of a molecule of triose. The energy required for the initiation of this cycle came from ATP and $\text{NADPH}^+ + \text{H}^+$ formed during the "light" reaction of photosynthesis.

The enzyme responsible for the primary carboxylation in photosynthesis is *carboxydismutase*. It also plays an important role in the reduction of carbon dioxide. According to Calvin one molecule of RuDP yields two molecules of 3-phosphoglycerate by addition of water according to the following scheme :



Reduction of CO_2 and synthesis of carbohydrates—PGA—the first stable triose sugar formed in the process of photosynthesis is immediately converted into phosphoglyceraldehyde (PGAlD) by reacting with NADPH formed in the "light" reaction. The enzyme which converts it is the *triose phosphate dehydrogenase*. Two molecules of PGAlD then react with *triose phosphate isomerase* and the two molecules unite head to head to form fructose 1, 6-diphosphate and then to fructose 6-phosphate.





The reaction of six carbon dioxide with six ribulose 1,5-diphosphate leads to the formation of a molecule of fructose 6-phosphate. Six molecules of ribulose 1,5-diphosphate are regenerated in the Calvin-Bassham cycle to keep the process going.

Fructose 6-phosphate is then converted to glucose 6-phosphate by *isomerase* and further to glucose 1-phosphate by the enzyme *phosphoglucomutase*. Glucose 1-phosphate then reacts with the nucleotide, uridine triphosphate (UTP)¹ in presence of enzyme *pyrophosphatase* and gives rise to uridine diphosphate glucose (UDPG).

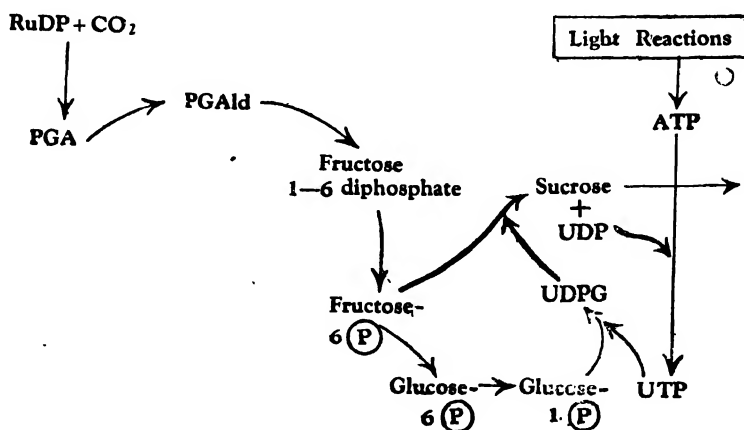
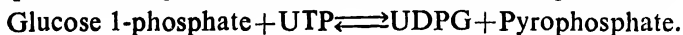


Fig. 9.6 Reduction of CO₂ and synthesis of carbohydrates.

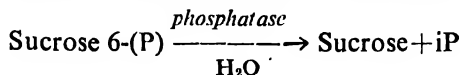
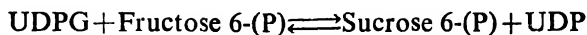
This UDPG is the precursor of UDP-xylose, UDP-arabinose, UDP-galactose (the various types of plant sugars responsible for the synthesis of cell wall) and also are responsible for the synthesis of

¹ It is formed by the union of uridine diphosphate (UDP) and adenosine triphosphate (ATP).

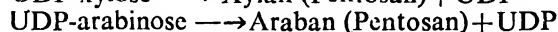
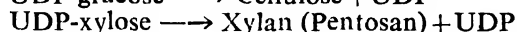
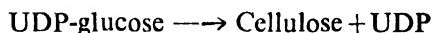
UDP is a complicated molecule formed by the union of uracil (a purine base) with two phosphate radicals and the pentose sugar ribose.

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hemicelluloses and pectins. UDPG is also involved in the synthesis of the very important plant disaccharide, sucrose by two reactions :

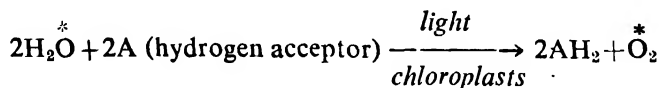


The synthesis of starches in plants proceeds either through glucose 1-phosphate and phosphorylase action or through UDPG and transglycosylase action. The synthesis of cellulose and pentosans in plants, however, takes place through UDPG and transglycosylase enzymes according to the following reactions :



The source of oxygen in photosynthesis—Another problem in the mechanism of photosynthesis is to find out the substance which is considered the most likely source of the process. Early view was that all the oxygen liberated in photosynthesis came from carbon dioxide but recently with the radioactive isotope it has been found that the oxygen liberated in this process comes from water and not from carbon dioxide.

Hill and others (1937 ; '39) demonstrated the evolution of oxygen when suspension of chloroplasts in water was illuminated in the presence of hydrogen acceptor. This phenomenon is known as *Hill reaction* which can be represented as



In this equation it has been shown by others that the oxygen liberated comes from the water molecule. It is now considered that the photocatalysed splitting of water into $[\text{H}^+]$ and $[\text{OH}^-]$ takes place in Hill reaction and helps in the formation of reducing substance which helps in the transference of hydrogen to carbon dioxide. The evolution of oxygen in the above experiment was noticed by Hill when leaf extracts or ferric salts were added. Thus in the presence of ferric salts or leaf extracts the chloroplasts were reduced and oxygen evolved without utilizing any carbon dioxide. From this, Hill concluded that chloroplasts contain a mechanism which absorbs light energy, reduces certain substances other than carbon dioxide together with the evolution of oxygen, this substance is concerned in the transference of hydrogen. The summary equation in the Hill reaction regarding carbon dioxide reduction is therefore

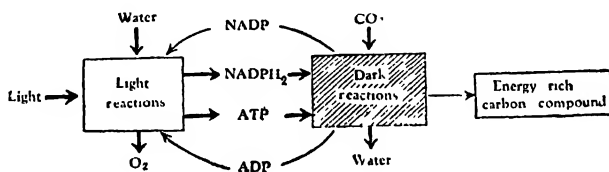


where (CH_2O) is the basic unit of the carbohydrate.

Hill's findings have been further supported by Ruben and Kamen (1941). By using *Chlorella* cells kept either (i) in water enriched with H_2^{18}O but with normal CO_2 as bicarbonates or (ii) normal water but with isotopically enriched C^{18}O_2 , they showed by means of mass spectrometric analysis that only when the $^{18}\text{O}_2$ was incorporated in water—the production of gaseous $^{18}\text{O}_2$ was quantitatively proportional. It proved more or less conclusively that oxygen evolved in photosynthesis was derived solely from water.

The OH^- donates an electron to the excited chlorophyll (refer *non-cyclic photophosphorylation*). The removal of an electron from OH^- converts it to a hydroxyl radical (OH) which combines with another radical to form a peroxide (H_2O_2). Subsequent decomposition of H_2O_2 yields molecular O_2 and H_2O .

The whole process of photosynthesis can therefore be summarily represented by the following diagram.



Evidences for the existence of light and dark stages in photosynthesis :

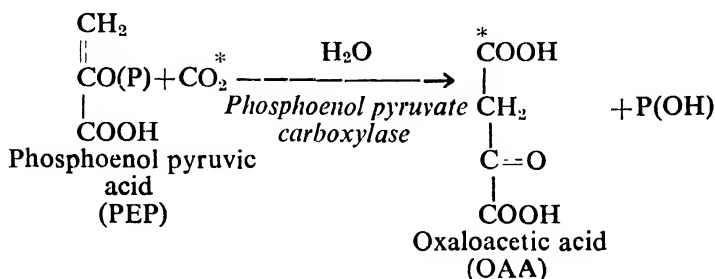
(a) *Intermittent light experiments* : Warburg (1919) showed that the rate of photosynthesis of a plant subjected to alternate light and dark stages was significantly greater than that of the plant kept in continuous light but receiving the same amount of total illumination as the former.

(b) *Temperature coefficient experiment* : Blackman, while studying the rate of photosynthesis observed that the temperature coefficient (Q_{10}) of a plant kept under intense illumination was always more than 2, while the Q_{10} of another set kept under light of low intensity was much less than 2 and often nearing unity. Blackman suggested the presence of a chemical stage in photosynthesis in addition to a photochemical stage. The chemical stage may be called the dark stage requiring no light.

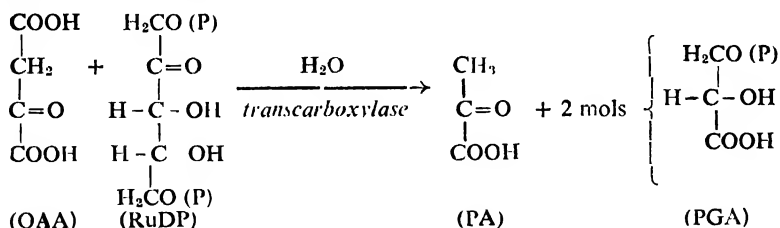
(c) *Dark fixation of carbon dioxide* : It has been demonstrated by subjecting suspensions of algae to high illumination in the absence of carbon dioxide and then rapidly transferring them to $^{14}\text{CO}_2$ containing medium in the dark—that the radioactive $^{14}\text{CO}_2$ has been incorporated in the system.

9.5 An alternate scheme for CO_2 fixation in Photosynthesis (Hatch and Slack pathway) : The universal operation of Calvin-Bassham cycle was questioned by two Russian workers, Tarchevski

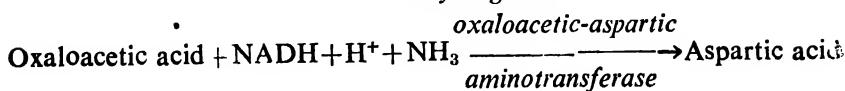
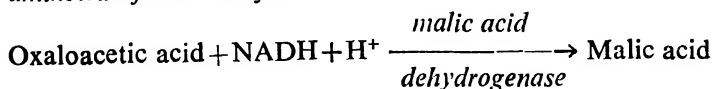
and Karpilov (1963). They observed that in corn (*Zea mays*) the first formed compound of photosynthesis belonged to the 4-carbon group e.g. malate and aspartate. Latter studies by Kortschak, Hartt and Burr (1965) also observed the similar observation of the previous workers. In 1966 Hatch and Slack reported that in sugarcane the first intermediate of photosynthesis is not a 3-carbon compound but four carbon dicarboxylic acid, oxaloacetic acid (OAA). According to them, the primary carboxylation takes place in the mesophyll cells in which the atmospheric CO_2 is accepted by phosphoenol pyruvic acid (PEP) rather than RuDP as in C_3 plants, to form C_4 dicarboxylic acid (OAA).



The enzyme responsible for this conversion is *PEP-carboxylase*. This 4-carbon compound (oxaloacetic acid) now combines with ribulose, 1-5 diphosphate (RuDP) to form 2 molecules of phosphoglyceric acid (PGA) and pyruvic acid (PA) is regenerated with the help of enzyme *transcarboxylase*.



The PGA is then transformed into various carbohydrates as in Calvin-Bassham cycle. Oxaloacetic acid may also be converted by side reaction into malic acid reacting with NADPH in the presence of *malic acid dehydrogenase* enzyme or into aspartic acid by reacting with NADPH and ammonia in the presence of *oxaloacetic-aspartic aminotransferase* enzyme.



The C_4 -dicarboxylic acid pathway has been well substantiated by subsequent data obtained by Hatch and Slack from enzyme studies and ^{14}C labelling patterns.

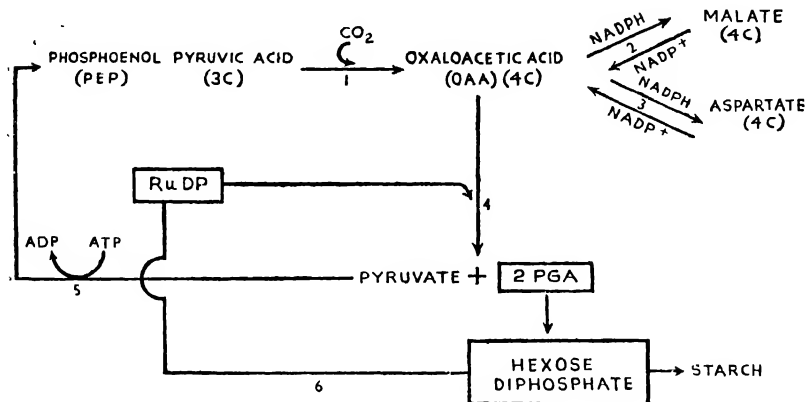


Fig. 9.7 Hatch and Slack pathway for CO_2 fixation. Enzymes involved (1) PEP-carboxylase, (2) Malate dehydrogenase, (3) Aspartate transaminase, (4) Transcarboxylase, (5) Phosphoenol pyruvate synthetase and (6) Calvin-Bassham cycle enzymes.

The Hatch and Slack photosynthetic pathway has been found in additional grass species which have originated in tropical climates. In addition to these grasses, some species of *Cyperus* (sedges) and of the dicotyledonous *Amaranthus* and *Atriplex* genera also depend primarily upon this pathway.

Considering the first formed product of photosynthesis by the two processes, (3-carbon compound-PGA or 4-carbon compound- OAA) higher plants are classified as C_3 and C_4 plants which is also referred to as Calvin-Bassham type & Hatch-Slack type plants respectively. They have got distinct anatomical, physiological and biochemical differences between them. Generally C_4 plants have high photosynthetic capacity than C_3 plants. It is because the temperature in the range of $32-35^\circ C$ is optimum in C_4 plants whereas the temperature threshold for C_3 plants is much less. C_4 plants photosynthesize much more effectively at low CO_2 conc. (due to the greater affinity of PEP-carboxylase than RuDP-carboxylase for CO_2). No detectable inhibition of photosynthesis have been observed by O_2 in case of C_4 plants whereas photosynthetic inhibition have been observed above 1% of O_2 in case of C_3 plants. C_4 plants have a well defined chloroplast-containing sheath of cells surrounding the vascular bundle, which may increase their ability to translocate carbohydrate. C_4 plants do not exhibit increased respiration rates in light or in the presence of O_2 (i.e. they lack photorespiration); low level of photo-

respiration results in maximum utilization of carbon skeletons for other metabolic processes. With all these above advantages the C_4 plants have a definite role in agriculture.

9.6 Enzymes in photosynthesis: Most of the information regarding the enzymes and enzyme system in photosynthesis has been derived from studies on the intact photosynthetic apparatus or from studies of partial reactions of photosynthesis (as in Hill reaction). Partial system i.e. Hill reaction most likely should be considered as multi-enzyme system in the sense of Dixon (1949).

Actually little information is available on specific enzyme system in photosynthesis. Enzymes which are responsible for glycolytic transformation of PGA into respiratory intermediates and sugar are not dealt here, although it is well realized that some of the intermediates of glycolysis may be of importance as precursor in the reaction system involved in photosynthetic carbon dioxide fixation.

(1) *Catalysts of the photochemical system :*

(a) *Chlorophyll as hydrogen-donor*—Chlorophyll may be considered as a photocatalyst concerned mainly with the transformation of light energy into chemical energy in the process of photosynthesis (Rabinowitch, 1945).

Frank and Herzfeld (1941) have postulated that chlorophyll in photosynthesis oscillated between an oxidised and reduced form denoting the reduced form as H-chlorophyll.

Recently Calvin and Aronoff (1950) suggested that chlorophyll functions through an enolizable hydrogen.

(b) *Catalyst B*—Frank and Herzfeld (1941) postulated a catalyst active in the stabilization of intermediate labile photoproduct. This has been termed as catalyst B. Cyanide has no effect on the working period of catalyst B and no known inhibitor is present for the activity of catalyst B.

(2) *Enzymes and co-enzymes involved in transfer of reducing energy to Hill oxidants*—In 1952 Ochoa and Stern suggested that co-enzyme I or II or both are the natural Hill oxidants in photosynthesis. They demonstrated that the isolated chloroplasts in the presence of pyridine nucleotide and proper enzyme and substrate carry out reductive carboxylation. This has been strongly supported later on by Frank and others.

(3) *Enzymes involved in carbon dioxide fixation*—The initial reaction of carbon dioxide fixation is a carboxylation reaction. Data from the isotopic experiments suggest that cyanide can inhibit this reaction. Frank and Herzfeld called this cyanide sensitive enzyme as catalyst A.

Specific enzymes which take part in carbon dioxide fixation are co-enzyme linked system active in reductive decarboxylation and carbonic anhydrase which takes part in photosynthetic reaction.

(a) *Carboxylases*—Clendenning, Waygood and others (1952) showed an enzyme responsible for decarboxylating PGA and found no evidence for direct or indirect decarboxylation through pyruvate. They also demonstrated the presence of other carboxylase enzymes in plants.

Fager (1952) however showed that addition of DPN or TPN had no effect on the light fixation of carbon dioxide in PGA.

(b) *Carbonic anhydrase*—It is one of the most important photosynthetic enzymes in plants. Its importance in photosynthesis is based on its general abundance in green tissues and its sensitivity to certain metabolic inhibitors which unfortunately are not specific for this enzyme. Carbonic anhydrase is inhibited by acid and sulfanilamide.

(4) *Enzymes relating to precursor of molecular oxygen :*

(a) *Catalyst C*—Frank and Herzfeld (1941) proposed that the enzyme catalyst C is active in the liberation of molecular oxygen from an intermediate peroxide.

(b) *Catalase*—It is said to be another oxygen liberating enzyme of photosynthesis present in higher plants. The strongest argument against this has been made by Gaffron (1937).

(c) *Hydrogenase*—Hydrogenase is an enzyme which reversibly catalyzes reactions involving molecular oxygen. Its occurrence in lower groups of plants is definitely established, but doubtful in higher plants.

(5) *Other enzymes :*

(a) *Cytochrome-f*—Hill and Scarisbrick showed the presence of cytochrome *f* in photosynthetic tissues. Hill in 1951 postulated that cyt. *f* could play a role in oxidative phosphorylation in photosynthesis. Its actual role in photosynthesis is still a matter of dispute.

9.7 Factors affecting photosynthesis : Like all physiological processes photosynthesis is conditioned by a number of factors. Some of which are external and some are internal. The most important external and internal factors which influence the rate of photosynthesis in plants are given below.

External factors :

1. **LIGHT**—It plays an important role in the rate of photosynthesis as the energy that is stored up in carbohydrate molecules during photosynthesis comes from light. Photosynthesis can be induced by any source of radiant energy which has wavelengths within the range of visible spectrum. In case of photosynthesis the main source of radiant energy under natural condition is the sunlight which may be direct or reflected. Light varies in *intensity*, *duration* and *quality*. When light falls on the leaves, a part is reflected, a portion is absorbed by the leaf and some quantity is transmitted through the leaf.

(i) *Effect of light intensity*—Generally the rate of photosynthesis is increased if the intensity of light is increased until some other factor e.g. carbon dioxide concentration becomes limiting. At low light intensity, the photosynthetic rate is more or less proportional to the light intensity if the carbon dioxide concentration is not the limiting factor. Again high light intensities inhibit the rate of photosynthesis. This phenomenon of inhibitory effect is known as *solarization*. It has been found (Holman, 1930) that if leaves are exposed to an illumination of 6800 foot-candles, starch formation takes place rapidly. On the other hand, if the value of the illumination is doubled, little starch accumulation takes place. The phenomenon of solarization is mainly due to *photo-oxidation*. In photo-oxidation oxygen is absorbed and used by leaves in presence of sunlight for the oxidation of some cell constituents and carbon dioxide is released in the process. The phenomenon of photo-oxidation though confused with the process of respiration still it is an entirely different process as photo-oxidation takes place with the mechanism of photosynthesis and also at higher rates than the mechanism of respiration. Hence photo-oxidation is regarded as variant of photosynthesis where oxygen is considered as harmful to photosynthetic organs if the process continues for a few hours.

Besides this, light also exerts direct and indirect effects on the rate of photosynthesis. At low light intensities stomata are closed and hence entrance of carbon dioxide is checked, consequently the rate of photosynthesis is decreased. Again as a result of high light intensities there is an increase in the transpiration rate which causes reduction of the water content in the cells of leaf, indirectly causing retardation in the photosynthetic rate. The chlorophyll which is necessary for the process of photosynthesis is destroyed by high light intensities.

(ii) *Effect of light qualities*—The effects of different light qualities on the photosynthesis have been studied by Hoover (1937), Gabrielsen (1948) and others. Hoover has found that maximum photosynthesis takes place at the red region of visible spectrum (wavelength 655 m μ) and the secondary maximum in the blue region having the wavelength 440 m μ . Gabrielsen on the other hand has shown that maximum rate of photosynthesis takes place in orange-red light, the secondary maximum in green-yellow light and lowest at the blue-violet light.

(iii) *Effect of duration of light period*—The rate of photosynthesis is also influenced if the duration of the light period is increased.

2. CARBON DIOXIDE CONCENTRATION—Generally an increase in the carbon dioxide concentration of the atmosphere results in an increase in the rate of photosynthesis until a point is reached when further increase in the concentration of carbon dioxide brings about no increase in the photosynthetic rate i.e., until other factors (like light) becoming limiting. If there is no limiting factor, the rate

of photosynthesis rises for a period with the increase in the carbon dioxide concentration. Again high carbon dioxide concentration retards photosynthesis. Stalfelt (1960) states that carbon dioxide inhibition is due to increased acidity of the mesophyll and perhaps a narcotic effect on the metabolic function of the cells. It has also been found that high carbon dioxide concentration may be responsible for the closing of stomata, the rate of photosynthesis is reduced as the carbon dioxide concentration of the assimilating cells is decreased; conversely low carbon dioxide values can accentuate the opening of stomata (Scarth and Shaw, 1951). In temperate regions during summer, the carbon dioxide concentration is generally the limiting factor in photosynthesis though the photosynthetic tissues are exposed to light. It has been found that increase in the carbon dioxide concentration of the atmosphere from its normal value (0.03 percent) has a good effect on photosynthesis as long as no other factors are limiting.

3. TEMPERATURE—It is rather problematic to study the effect of temperature on photosynthesis as in case of land plants it is difficult to maintain the temperature at a desired value when they are exposed to light. Photosynthesis can take place within a wide range of temperatures. In some conifers it has been found that photosynthesis occurs at -35°C while in case of lichens the process takes place at -20°C .

In case of tropical plants high temperature is essential for an increase in the rate of photosynthesis while temperate plants require temperature as low as -6°C . Generally the rate of photosynthesis is increased up to a point when other factors like carbon dioxide concentration, light etc. are not limiting. If the temperature is increased further, rapid decline in the photosynthetic rate resulting in injurious effect on the protoplasm takes place. It has been pointed out by several investigators that at higher temperature the photosynthetic rate decreases with time—this is due to some internal factors, generally called *time factor*.

The optimum temperature for photosynthesis varies considerably within the range of 25° – 30°C . Photosynthesis shows progressive increase with rise of temperature and follows Van't Hoff's rule. The light step being a physical reaction (at least initially) will have a temperature coefficient¹ (Q_{10}) near 1.0 and the dark reaction will

¹ **Temperature Coefficient (Q_{10})**—The influence of temperature on the rate of biological processes is extremely important. Most of the processes in the living plant cells are the result of series of chemical reactions, the velocity of which is related to temperature according to Van't Hoff's law. This effect of temperature is conveniently termed as **temperature coefficient** or more commonly as Q_{10} . It is the ratio of the reaction rate (velocity) at 10°C higher by the velocity at particular temperature.

$$\text{Temperature coefficient} = \frac{\text{Velocity at } (T^{\circ} + 10^{\circ})}{\text{Velocity at } T^{\circ}}$$

When acting directly, a rise of temperature by 10°C usually causes a doubling or trebling of the rate of biological activity and is said to have a Q_{10} 2 or 3. With

have a Q_{10} above 2.0. Most reports indicate that the Q_{10} values for photosynthesis lie between 1.0 and 2.7.

4. *Oxygen concentration*—An inhibitory effect on the rate of photosynthesis has been found to take place in most of the terrestrial plants that are exposed to high oxygen concentration of the atmosphere. Generally the photosynthetic rate is decreased if there is an increase in the oxygen concentration. This is due to the fact that the enzymes responsible for photosynthesis act in a reverse direction if there is greater amount of oxygen. Hence oxygen exerts a direct inhibitory effect upon photosynthesis.

5. *Water supply*—Water plays an indirect role in photosynthesis as very small percentage of the absorbed water is utilised in photosynthesis. Still it has been found that reduction in the water content of leaves results in the reduction of the photosynthetic rate, which probably is due to (i) its control of stomatal opening and its effect on wilting of leaves and (ii) decrease in the percentage of water of chloroplasts and also other parts of protoplasm.

6. *Chemical compounds*—Several chemical compounds like chloroform, ether, hydrogen sulphide, quinine, hydrocyanic acid etc. have direct or indirect effect upon the photosynthetic rate when they are absorbed in little quantities. This is due to the fact that these chemical substances inhibit the activities of the enzymes responsible for photosynthesis.

7. *Age effect*—With age the ability of the individual leaves to photosynthesize depreciates considerable. This has been shown with perennial leaves like conifers and palms. Here the photosynthetic rates are highest at leaf maturation and gradually decline during successive years. Even in annuals this kind of decline has been shown with age. The main reason for such decline is due to deterioration of the anabolic activities which results in the senescence of leaves (Das and Leopold, 1964).

Internal Factors :

8. *Chlorophyll content*—Although chlorophyll is essential for photosynthesis, still it has been shown by a number of workers that there is practically no proportional relationship between photosynthe-

physical reactions such as diffusion and photodriven reactions the Q_{10} is relatively low (1.2 to 1.4). For enzymatic reaction the Q_{10} values may be higher (1.3 to 5.0 and usually they range around 2). As majority of the biological activities are catalyzed by enzymes, Van't Hoff's law is applicable to these bioprocesses within the temperature range of 0° to 30°C. Above 30°C the reaction rate declines dramatically and the Q_{10} values decreases from 2 to nearly 1. Van't Hoff's law is not applicable at higher temperature (above 30°C) as enzyme inactivation takes place more rapidly at higher temperature than their effect on the velocity of the biological processes. At the higher level (above 25°C) the Q_{10} values must be carefully interpreted particularly with attention to the effect of time. For the rate or reaction may be doubled between 20°C to 30°C for a period of 2 hours, but if continued for several hours, the rate will decrease.

sis and chlorophyll content in the leaves of plants. Willstätter and Stoll (1918) have studied this relationship with the help of photosynthetic number; the *photosynthetic number* "is the number of grams of carbon dioxide absorbed per hour per gram of chlorophyll."

Deficiency of some inorganic nutrients like iron, sulphur, nitrogen and magnesium can bring about limitations of photosynthesis through the depression of the chlorophyll content of leaves (Kennedy, 1940).

9. *Protoplasmic factor*—Protoplasm plays an important role in the increase of photosynthetic rate because of the water content and the presence of various kinds of enzymes in protoplasm.

10. *Accumulation of the end products*—Photosynthesis is retarded if the end products like carbohydrates are accumulated in the photosynthesising cells. Hence the rate of photosynthesis is inversely proportional to the concentration of the end products.

11. *Anatomical structure of leaves*—The photosynthetic rate is greatly influenced by the internal structure of leaves (e.g. the size and structure of stomata, distribution of intercellular spaces, arrangement of palisade and spongy layers, presence of non-green mesophyll tissues etc. influence the rate of photosynthesis). The entrance of carbon dioxide and penetration of light to chlorenchyma cells also affect the photosynthesis in plant organs.

9.8 The principle of limiting factor : While studying the effect of different environmental factors like light intensity, carbon dioxide concentration, temperature etc. most of the physiologists tried to

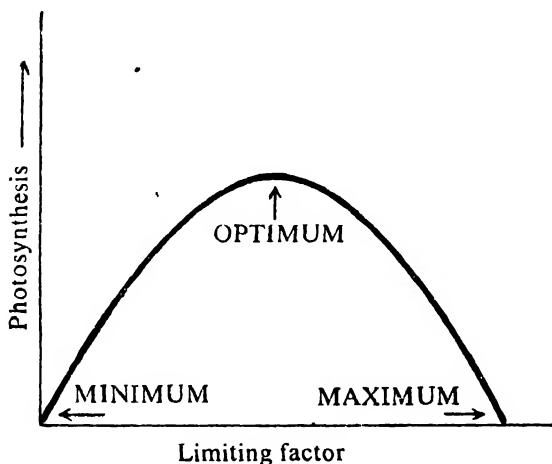


Fig. 9.8 Graphic representation of three cardinal points.

study the effect independently of the other factors. Thus any of the factors can be *minimum*—where the process just started and a *maximum*—where the process comes to an end. Different workers

obtained different values and an anomalous situation arose in the values of *optimum*. It shows that the optimum value for any particular factor can be altered by changing other factors. Thus optimum carbon dioxide value was found to be greater at high light intensities than at low ones. Similarly optimum temperature varies with light intensity.

The first important clarification of the problem was made by Blackman (1905) who enunciated the **principle of limiting factors** based on Liebig's "law of minimum". According to Blackman, "when a process is conditioned as to its rapidity by a number of separate factors, the rate of the process is limited by the pace of the 'slowest' factor."

As for example, suppose that the intensity of light is sufficient so that, at the most 5 ml of carbon dioxide can be utilised by a particular leaf in an hour during photosynthesis; but if 1 ml of carbon dioxide is allowed to the leaf in an hour, then the rate of photosynthesis is limited by carbon dioxide factor. As carbon dioxide is increased, the rate of photosynthesis is increased until 5 ml of carbon dioxide is utilised by the leaf in an hour. If carbon dioxide supply is increased more than 5 ml then there will be no increase in photosynthesis due to insufficient light. In this case light is the limiting factor.

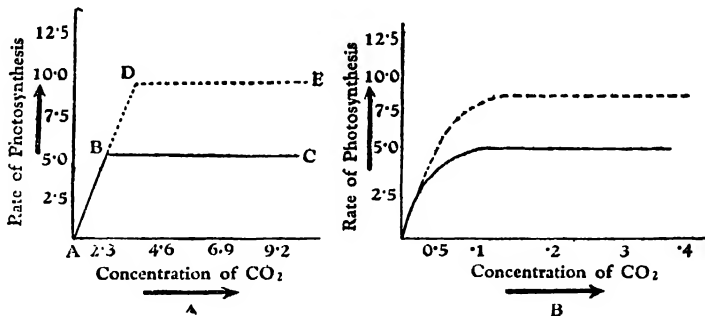


Fig. 9.9 Graphs illustrating the principle of limiting factors in photosynthesis. A—Blackman's original interpretation. B—Interpretation of later workers (James, Harder etc.)

Blackman illustrated his law of limiting factor by graphical representation (Fig. 9.9A). In this graph the abscissa represents different carbon dioxide concentration while the ordinate represents the rate of photosynthesis. Here light intensity is kept constant at the point A and carbon dioxide concentration increased from 0.0 to 3.0, 3.0 to 4.0; but the rate of photosynthesis will not increase due to the increase of carbon dioxide concentration beyond A. So the rate of photosynthesis will be constant along the abscissa. Again if the light intensity is increased so as to utilize 3.0 ml of carbon dioxide by the leaf then the rate of photosynthesis will also increase and reach up to

the point B (where it stops) and becomes constant along BC parallel to the abscissa. If light intensity is sufficient to utilize 4.0 ml of carbon dioxide concentration, the rate of photosynthesis will increase upto D and then will be parallel to the abscissa along DE.

In case of the process of photosynthesis, light and carbon dioxide are not the only factors that can be limiting but any other factors that influence the photosynthesis also may become limiting.

The idea of limiting factors proposed by Blackman was not accepted by Harder, James and others in such a simple way. They have found that when photosynthetic rates are plotted together with the corresponding variation in some other factors along the abscissa then instead of abrupt changes in the resulting curve to a horizontal position (Fig. 9.9 A), a gradual transition to a position more or less parallel to the abscissa results (Fig. 9.9 B).

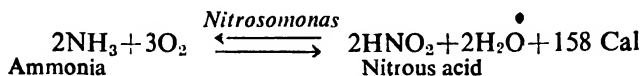
The gradual transition instead of sudden change in the curve as postulated by Blackman was explained on the basis of the fact that there are huge number of chloroplasts—the seat of photosynthesis, even in a small leaf. All chloroplasts are not equally subjected to the same intensity of light, nor they can utilize the same amount of carbon dioxide. As light and carbon dioxide become limiting factor the rate of photosynthesis is checked in some chloroplasts sooner than in others. For this the fall in the photosynthetic rate in the curve will be gradual instead of abrupt, because while the process of photosynthesis though stops in some chloroplasts as a result of some limiting factors, but continues in other chloroplasts where any factor is not becoming limiting.

It is evident from the above facts that the term 'limiting factor' does not mean the absolute minimum quantity of a particular factor in relation to other factors but their relative minimum quantity practically required in the process.

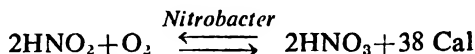
9.9A. Chemosynthesis: The utilization of the energy of the sun in photosynthesis has been made only by the green plants. The synthesis of organic food stuff is, however, not a monopoly of green plants alone. But there are some lower groups of plants and bacteria which can manufacture or synthesize their food without utilizing light as a source of energy; instead they obtain their necessary energy by the oxidation of some chemical elements like ammonia, hydrogen sulphide etc. This mode of synthesis, where the energy required for the synthesis of food from carbon dioxide and water comes from chemical substances and one kind of energy is transformed into another is known as *chemosynthesis*.

(1) *Nitrifying bacteria*—There are several groups of autotrophic chemosynthetic bacteria of which the most important are the nitrifying bacteria. These are colourless, aerobic bacteria which synthesize carbohydrates using energy derived from oxidative reactions rather than radiant energy. According to Winogradsky (1889) the oxidation takes place by the action of two kinds of bacteria viz., (i) *Nitroso-*

monas, *Nitrosocystis*, *Nitrosospira* etc. and (ii) *Nitrobacter* and *Bactoderma*. The first group of nitrate bacteria is the small mobile cocci that oxidise ammonia to nitrous acid according to the following equation.



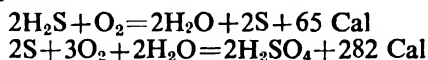
The latter group further oxidises nitrous acid into nitric acid according to



By the oxidation of nitrogenous organic compound as their source of energy and using carbon dioxide as a source of carbon, the nitrifying bacteria do not require any other organic compound as respiratory material.

Nitrifying bacteria represent a special physiological type, sharply differing from the green autotrophic plants as well as from the usually colourless heterotrophic saprophytes and parasites. Between photosynthesis and respiration the contrast is not very distinct in this type of bacteria. The energy of the exothermic process of oxidation of ammonia into nitrous acid is used by this bacteria both for the synthesis of organic substances and for the maintenance of other vital processes as growth, movement etc.

(2) *Colourless sulphur bacteria*—Like nitrifying bacteria, sulphur bacteria also obtain their energy from H_2S and other compounds containing reduced sulphur. These bacteria (e.g. *Beggiatoa*, *Thiobacillus*, *Thiothrix*) live in the thermal springs and oxidise hydrogen sulphide to sulphur and further to sulphuric acid according to the following equation.



The energy released by these bacteria is utilised in the decomposition of carbon dioxide. Sulphur bacteria are of various types. Some are known as purple bacteria because of the presence of purplish red pigment—*bacteriopurpurin*. Engelman is of opinion that this pigment substitutes the chlorophyll and participates in the photodecomposition of carbon dioxide.

According to Park (1963) the photosynthesis in this bacteria is similar to that of higher plants except that the hydrogen 'donor' is not water but hydrogen sulphide (H_2S). The equation is given below



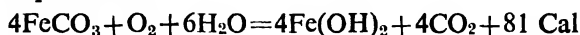
and 6 molecules of this



Oxygen is not liberated in the process and a considerable amount of energy is set free during the oxidation process—a part of which is

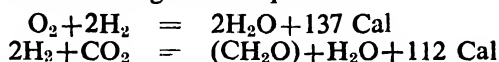
heat energy and a part is chemical energy which is used in the conversion of carbon dioxide and hydrogen sulphide into carbohydrate.

(3) *Iron bacteria*—Iron bacteria (e.g., *Leptothrix ochraceae*, *Ferrobacillus*, *Spirophyllum ferrugineum*) which live in water and obtain energy due to conversion of ferrous salts or ferric salts by the oxidation processes.



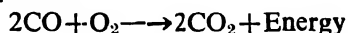
The energy released is used in the manufacture of the carbohydrates.

(4) *Hydrogen bacteria*—There are certain bacteria (e.g. *Bacillus pantotrophus*) which live saprophytically in the soil and can grow artificially in medium containing hydrogen, oxygen, carbon dioxide. Ruhland (1936) found that this bacteria can oxidise hydrogen with the liberation of energy which is then utilized for the chemosynthesis of organic food according to the equation.



The energy liberated may be utilized in the synthesis of carbohydrate and the process is similar to that proceeds in green photosynthesizing cells.

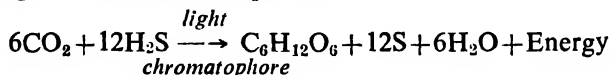
(5) *Carbon bacteria*—It oxidises CO into CO_2 according to the following equation



The energy then utilizes in the synthesis of carbohydrate and other organic compounds.

B. Photosynthetic bacteria (Bacterial photosynthesis) : Besides chemosynthetic bacteria there is another group of bacteria known as *photosynthetic bacteria* which can synthesize carbohydrate using light as a source of energy. They usually grow in a place where the compound which serves as hydrogen donor occurs. The following are the important photosynthetic bacteria :

(1) *Green sulphur bacteria*—The most important genus of the green sulphur bacteria (Chlorobacteriaceae) are *Chlorobium* and *Chlorobacterium*. They contain the most important pigment—*bacterioviridin* or *bacteriopurpurin* which is similar to chlorophyll. The most important photosynthetic activity of this group of bacteria is the photoreduction of carbon dioxide in the hydrogen sulphide medium according to the following equation.

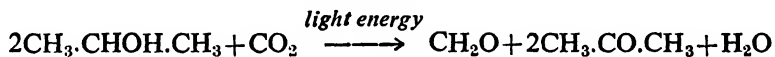


In contrast to the process of photosynthesis in higher green plants, this reaction indicates that this group of bacteria liberates energy and the process of reaction is exothermic whereas in higher green plants it is endothermic. Like blue-green algae, *Chlorobium* is anaerobic in nature and can fix considerable amount of atmospheric nitrogen.

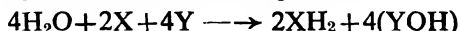
(2) *Purple sulphur bacteria*—The second group of photosynthetic bacteria is the purple sulphur bacteria (Triorhodaceae) which contain the characteristic pigment—*bacteriochlorophyll*. The bacteria (*Chromatium*) usually react on a variety of sulphur compounds, molecular hydrogen and sometimes selenium compound for the reduction of carbon dioxide. The important overall chemical reactions caused by this group of bacteria are given below.



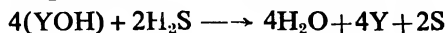
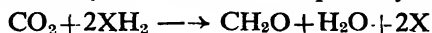
(3) *Purple non-sulphur bacteria*—The most important purple non-sulphur bacteria (Athiorhodaceae) is *Thiorhodaceae* which can live in presence of organic acids, alcohol etc. The bacteria oxidises organic compounds with simultaneous reduction of carbon dioxide. The reduction of carbon dioxide always takes place in presence of light absorbed by the pigments. Photoreduction of carbon dioxide takes place with the substrate alcohol and the energy is obtained mainly from sun light (infra red) absorbed by the purple pigment—*bacteriochlorophyll*. The reaction for the reduction of carbon dioxide by this bacteria takes place according to



The amount of light quanta required for the reduction of one molecule of carbon dioxide is the same as that takes place during photosynthesis in higher plants. It clearly indicates that in all these organisms the primary photochemical reaction is the same. The mechanism of photosynthesis for these bacteria is the formation of a "hydrogen donor" which ultimately supplies this hydrogen for the reduction of carbon dioxide. Due to removal of [H] from the water there is formation of OH radical and in this bacteria the fragment of the water molecule is reduced by the hydrogen donor such as H_2S . So the primary reaction of these organisms



Where 'X' and 'Y' are the acceptors of H and OH ions respectively. The subsequent reaction for photosynthesis will therefore be



So, considering all the foregoing discussion van Neil proposed the general equation



which shows that the photoreduction during normal photosynthesis is same as the chemoreduction of carbon dioxide by photosynthetic bacteria. According to van Neil bacterial photosynthesis does not involve the production of oxygen. He further showed that when H_2A is H_2S or alcohol, A will be represented by sulphur or acetone

respectively, if it is the case of a molecular hydrogen there will be no existence of A.

The photosynthetic bacteria that use the external hydrogen donors H_2 and H_2S are able to reduce $NADP^+$ independent of light. The high reducing capacity of such donors permits the direct transfer of

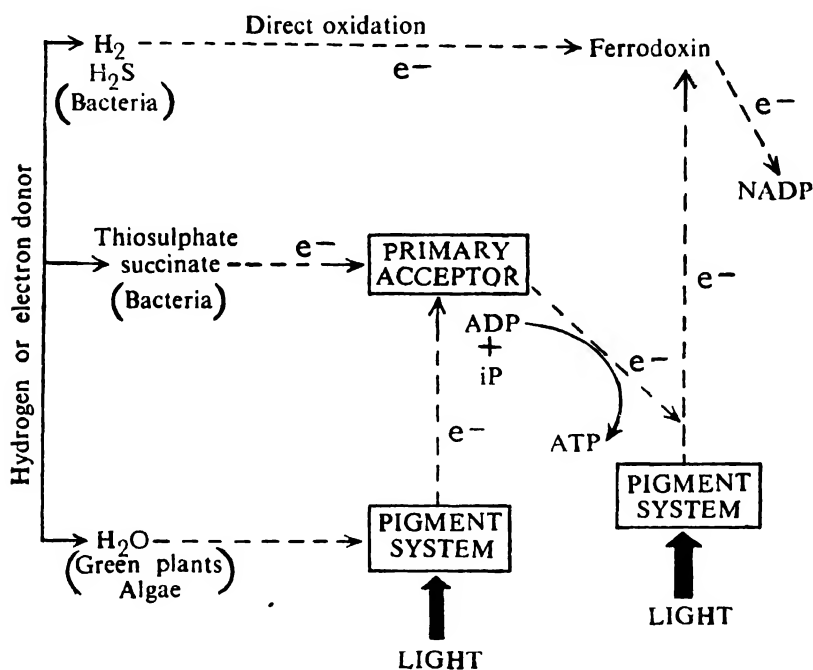


Fig. 9.10 Comparison of photosynthetic process in bacteria, blue-green algae and cells of higher plants.

hydrogen to $NADP^+$ without the expenditure of light energy. Many of these bacteria also utilize inorganic thiosulphate and organic substances such as succinate as hydrogen sources. Light activation of bacteriochlorophyll system results in the transfer of electrons from this system of $NADP^+$, thereby promoting the removal of electrons from thiosulphate or succinate via a series of electron carriers. In this way light energy generates a flow of electrons from

Donor \rightarrow Cytochromes \rightarrow Chlorophyll \rightarrow $NADP^+$

The mechanism employed by green plants to photoreduce $NADP^+$ would seem to be a logical extension of this type of bacterial photoreduction. A comparison of the steps involved in the photoreduction of $NADP^+$ by bacteria and the cells of higher plants is shown in Fig. 9.10.

9.10 Measurement of photosynthesis—Since the most important life process of the plant—photosynthesis, consists of a chain of reactions and occurring in a place which is also the site of hundreds of such chemical reactions, the way to measure photosynthesis is therefore very complicated. The most important process which can hamper the process of photosynthesis is respiration, as the process is involved in the oxidation of part of the carbohydrate produced in photosynthesis. Therefore the quantity of photosynthate produced in a particular time is always less than the true value and is said to be *apparent* or *net photosynthetic rate*. Since the process of respiration is insignificant as compared with the process of photosynthesis, the difference between the apparent value and the true value of photosynthesis is always insignificant and therefore the apparent value should be considered as the basis for determining the rate of photosynthesis.

There are three general methods for the quantitative determination of photosynthesis. These are (a) estimation of the amount of oxygen evolved in photo-

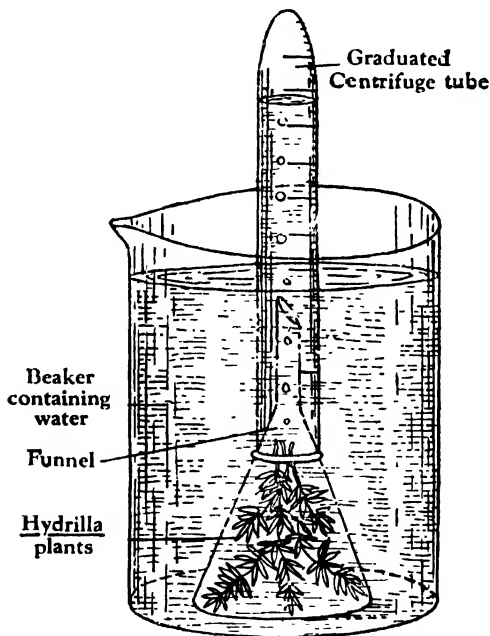
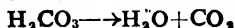
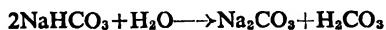


Fig. 9.11 Experiment demonstrating the evolution of oxygen in photosynthesis.

synthesis; (b) estimation of carbon dioxide absorbed in photosynthesis and (c) determination of dry weight increase of the photosynthesizing organs.

(a) *Estimation of amount of oxygen evolved*—A large beaker of 500 ml capacity is taken and filled up to $\frac{2}{3}$ rd its capacity with distilled water containing 0.1% NaHCO_3



solution (as a source of carbon dioxide). Immerse some *Hydrilla* plants in the beaker with their cut ends of the stems up. Invert a short-stemmed glass funnel over the plants in the beaker in such a way that the limb of the funnel almost

covers up the *Hydrilla* plants and the stem of the funnel should be about 1 cm under the surface of water. Invert a graduated centrifuge tube (10 to 20 ml capacity) filled with water over the stem of the funnel carefully (Fig. 9.11). The whole apparatus is now exposed to bright light and observed from time to time for evolution of bubbles from the cut ends of the plants which will collect in the test tube by the displacement of water.

The gas that collects at the top of the centrifuge tube is oxygen, which can be proved by the fact that it can rekindle a glowing chip. Further, by adding potassium pyrogallate solution¹ the level of water in the centrifuge tube is found to be gradually rising upwards due to absorption of oxygen.

The main drawback of this method is that the oxygen evolved is not in a pure form but mixed with other gases like carbon dioxide and nitrogen.

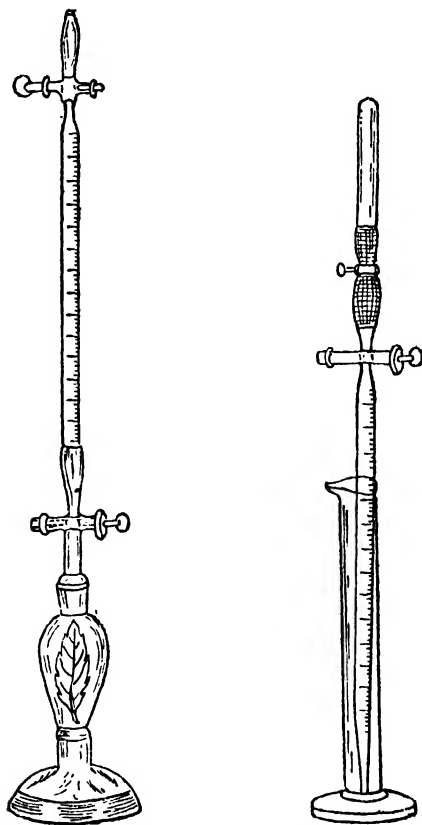


Fig. 9.12 Ganong's photosynthometer.

(b) *Estimation of the amount of carbon dioxide absorbed*—The amount of carbon dioxide absorbed in photosynthesis can be calculated by *Ganong's photosynthometer*. It consists of three parts : (a) a glass bulb, (b) a graduated tube

¹ Prepare the solution by combining 1 part of weight of pyrogallic acid, 5 parts of potassium hydroxide and 30 parts of water.

and (c) a connecting link (Fig. 9.12). The volume of the whole set when fitted is a little over 100 ml (i.e. 103 ml).

Now introduce a few fresh green leaves with small amount of water (the volume of the leaves and water should be 3 ml) within the lower bulb of the apparatus. The volume of the apparatus, therefore, stands as 100 ml of air.

The graduated tube is inverted and filled upto 5 ml mark with water. Close the stop cock and fit it with the connecting link (c). Now close again the stop cock of (c) and fill the other hollow end of this link with water and closing it with the hand invert in into a beaker containing water. Clamp the set and keep the level of water in the beaker upto the hole (h) of the connecting link. Now connect the top of the graduated tube to a CO_2 -generator (Kipps apparatus). Open the lower and upper stop cock and admit carbon dioxide. The water will gradually flow down the graduated tube and filled up by carbon dioxide. The top stop cock is closed when the level of water in the graduated tube falls to the level of the water outside. The tube now contains 5 ml of carbon dioxide. The whole set is now fitted at the top of the glass bulb. So that the holes ($h+h'$) lie opposite each other, so that the pressure is at atmospheric pressure. Now twist the connecting link slightly so that the holes ($h+h'$) lie well apart and all connections are made airtight. Open the lower stop cock so that carbon dioxide will diffuse to the bulb. Now keep the whole set in light for several hours.

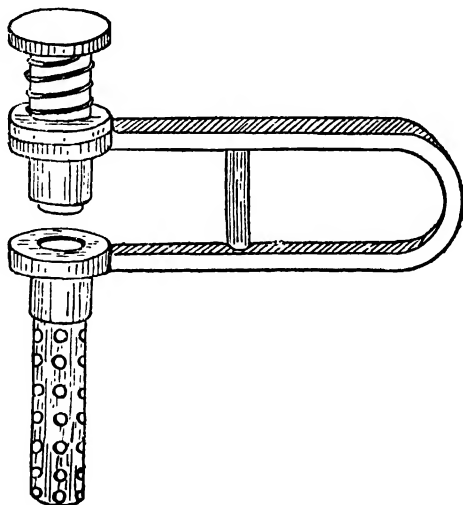


Fig. 9.13 Ganong's leaf cutter.

After the experimental period close the stop cock of (c) and remove the upper part and place it in a beaker containing water. Now remove the connecting link under water. Connect the tube containing 30% KOH solution with end of the graduated tube through a rubber tubing. Lift the tube from the beaker and close the lower end with a finger. Open the upper stop cock and allow the caustic potash to enter the tube. After shaking the tube with KOH, immerse it into a breaker of water (at the same level). The water will rise in the tube and from this rise the percentage of unused carbon dioxide can be calculated. The difference between the actual amount of carbon dioxide at the beginning of experiment and the amount of unused carbon dioxide gives the actual amount of carbon dioxide utilized in photosynthesis.

This experiment is slightly erroneous as carbon dioxide is slightly soluble in water.

(c) *Dry weight increase in photosynthesis*—Since the process of photosynthesis causes an increase in the accumulation of carbohydrate, the rate of the process can be determined by finding the increase in the dry weight of the material. This method has been improved by Thoday and Ganong. It consists of cutting a number of discs (75-100 disks) from a part of the leaf in the morning hour (so that the leaf is starch free¹) by means of *Ganong's leaf cutter* (Fig. 9.13). These discs are then transferred to an oven and dried (usually by increasing the temperature upto 100-110°C) to a constant weight. Keep the other part of the leaf under normal illumination in daylight. After a period of illumination (i.e. towards the evening) cut equal number of discs from same leaf and dry it as before.

The gain in the dry weight is said to be due to accumulation of sugar during photosynthesis and is said to be the value of apparent photosynthesis.

9.11 Experiments on photosynthesis :

(i) *Demonstrate experimentally the necessity of light in photosynthesis.*

A well grown potted plant whose leaves are made starch free¹ is taken. A starch free leaf is then covered with *Ganong's light screen*. The main advantage of this screen is that a part of the leaf is cut off from the light without any hindrance to its ventilation.

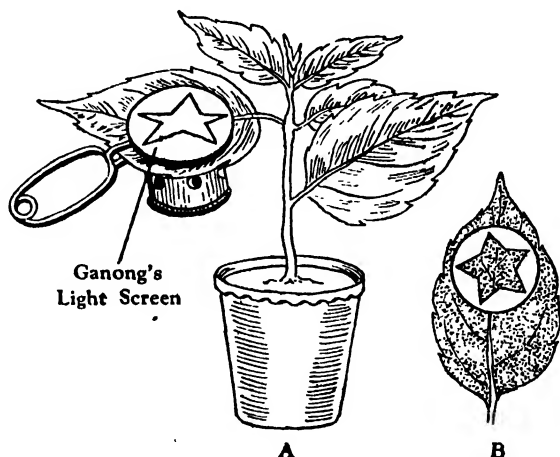


Fig. 9.14 Experiment to show that light is necessary for photosynthesis by Ganong's light screen.

The whole plant with the light screen attached to one of its leaf is then kept in light. After 24 hours the screen is taken off and the leaf is detached from the plant and it is then bleached with 95% hot alcohol. After its complete decolourisation the leaf is washed with water and treated with iodine. The exposed part of the leaf appears blue showing the formation of starch whereas the covered portion where light can not penetrate is yellowish, showing that no starch formation has taken place there (Fig. 9.14).

(ii) *Demonstrate experimentally the necessity of carbon dioxide in photosynthesis.*

No photosynthesis can take place in an atmosphere completely devoid of carbon dioxide ; that can be proved by Moll's experiment.

¹ The leaves are made starch free by keeping the plant in darkness for 24 hours.

A wide mouthed bottle whose mouth is fitted with a split cork is taken, A small quantity of 2% KOH solution is introduced in the bottle and the bottle is placed horizontally on a tripod stand. A starch free leaf from a healthy potted plant is introduced through the split of the cork so that half part remains inside the bottle and the other half out side as in Fig 9.15. All connections are made airtight with vaseline and the whole set is placed in direct sunlight. After 24 hours the leaf is detached from the plant and is taken out from the bottle. The leaf is then bleached with boiling alcohol and is treated with iodine [refer experiment (i)]. The portion of the leaf remaining outside the bottle receives all conditions for photosynthesis and so starch formation takes place normally there, as it is evident from the blue colouration with iodine. The other half which remains inside the bottle where no carbon dioxide is available (due to absorption by KOH solution) turns yellow showing no starch formation.

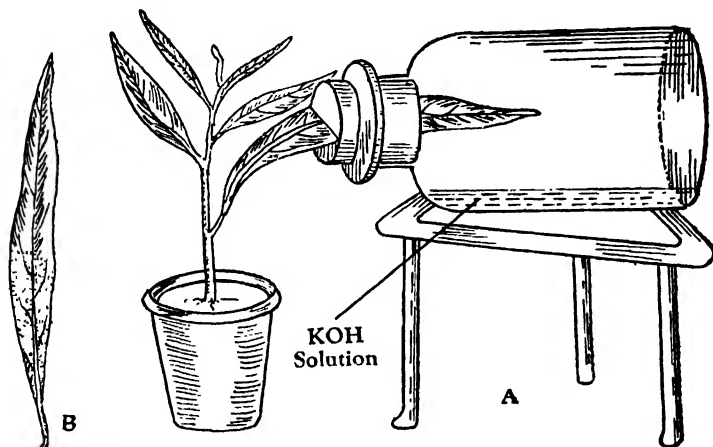


Fig. 9.15 Moll's experiment to show that carbon dioxide is necessary for photosynthesis.

(iii) *Demonstrate experimentally the necessity of chlorophyll in photosynthesis*—Without chlorophyll no photosynthesis takes place and this can be proved by keeping a *Coleus* plant (which has variegated leaves—the central portion of this leaf is red and does not contain chlorophyll) in darkness for making it starch free. Now a suitable leaf is selected and the green regions near the edge are marked. Then the plant is exposed to sunlight for few hours. After this, the leaf is treated with iodine solution after proper decolourization. It will be found that the marginal portion of the leaf turns violet-blue, the central portion remains unstained. This is a proof that the middle chlorophyll-less portion produces no starch indicating thereby that chlorophyll is necessary for photosynthesis.

(iv) *Demonstration of evolution of oxygen in photosynthesis.*

(a) refer article 9.10 (a).

(b) *Oxidation-reduction method to prove the production of oxygen in photosynthesis.*

Reduced indigo carmine is very effectively used to demonstrate the evolution of oxygen. 0.01% of indigo carmine is prepared with tap water. This will give a bright blue colouration. Prepare a 10% solution of sodium hydrosulphite ($\text{Na}_2\text{S}_2\text{O}_4 \cdot 2\text{H}_2\text{O}$) in tap water. Add drop by drop the latter solution to the indigo carmine solution carefully, so that it (indigo carmine solution) becomes completely reduced as indicated by the disappearance of blue colour to white. Care should be taken not to add an excess of even a drop of sodium hydrosulphite.

Carefully fill this reduced solution to a test tube (avoiding air to come in contact with the solution as far as possible) if any considerable blueing takes place in the mean time, add a minute drop of sodium hydrosulphite to make it colourless again.

Introduce some small *Hydrilla* plants to the test tube and invert the test tube in a beaker containing reduced indigo carmine solution.

Now keep the whole set in bright sun light and within a few minutes the solution will turn blue due to reoxidation of the indigo carmine solution by the oxygen evolved in photosynthesis.

A control set placed in the dark shows no oxidation and consequently no change in colour of the solution was observed.

9.12. Carbon cycle : The sources of carbon dioxide required by green land plants are the carbon dioxide gas, carbonic acid or other inorganic or organic salts. Aquatic submerged plants get carbon dioxide, present in water in dissolved condition. Green plants are continually removing atmospheric carbon dioxide during the process of photosynthesis resulting in the deficiency in the total atmospheric carbon dioxide concentration. Again to maintain the proper balance, carbon dioxide is released to the atmosphere by the respiration of plants and animals. When organic residues of plants and animals are decomposed by the activities of bacteria and fungi, the carbon is released in the form of carbon dioxide which escape into the atmosphere. As a result of "soil respiration" influenced by the microorganisms, carbon dioxide gas from the soil evolves – due to this soil respiration, greater amount of carbon dioxide is returned to the atmosphere.

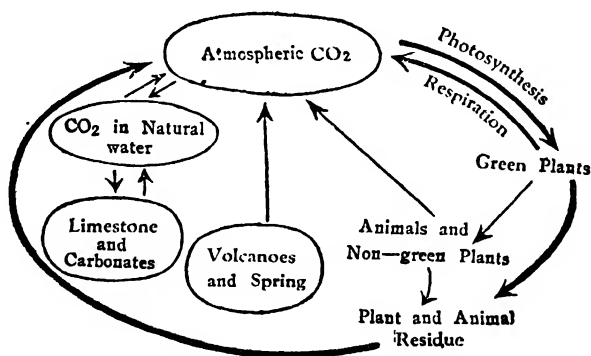


Fig. 9.16 Carbon cycle.

Other sources of atmospheric carbon dioxide are volcanoes, springs, and some fuel materials. The total amount of carbon released from the above is very little. At the time of burning of coal, gasoline, wood, oil etc., carbon dioxide is released to the atmosphere.

Huge amount of carbon dioxide is found more in oceans than the atmosphere. Carbon dioxide is utilised by marine plants during photosynthesis which is again released at the time of respiration.

Many marine animals take marine plant as their food. During the process of respiration a small amount of carbon in the food is released as carbon dioxide in the water. In the shells of some marine animals large amount of carbonates is present. The carbon dioxide content of the water increases when bicarbonates are converted into carbonates together with the release of carbonic acid. At the time of the dissolution of rocks of limestones, carbon dioxide (that are tied up in the form of carbonates) is released into the atmosphere or dissolved in water.

The carbon cycle in nature is shown in Fig. 9.16.

SELECTED QUESTIONS

1. What is photosynthesis? Give a brief historical sketch of the discovery of the process.

Refer articles 9.1 and 9.2

2. Describe in brief the mechanism of photosynthesis.

Refer article 9.4

3. How does green cells absorb light? Discuss the mechanism of energy transfer in different plant pigment molecules.

Refer topic *the conversion of light energy to chemical energy* in article 9.4.

4. Differentiate between cyclic and non-cyclic photophosphorylation. Assess their relative role towards the conversion of light into chemical energy.

Refer topic *the conversion of light energy to chemical energy* in article 9.4

5. What are 'light' and 'dark' reaction? Adduce evidences to show the existence of these two phases in photosynthesis.

Refer topic *'light' and 'dark' reaction* in article 9.4 and add also the *evidences for the existence of these two phases* in the same article.

6. Describe the source of oxygen in photosynthesis or Hill reaction and its significance.

Refer topic *the source of oxygen in photosynthesis* in article 9.4

7. "Photosynthesis can be placed alongside with other oxidation-reduction reactions"—Discuss.

Refer article 9.4

8. Give an account of the enzymes involved in photosynthesis.

Refer article 9.6

9. Describe the role of tracer technique in the elucidation of the mechanism of photosynthesis.

For the tracer technique refer chapter 1 article 1.5 and for its role in photosynthesis refer article 9.4.

10. Discuss the effect of external factors in photosynthesis.

What principles were enunciated to explain the interaction of these factors on the process.

For first part of the question refer article 9.7 and for the last part refer article 9.8.

11. What are the internal factors that influence photosynthesis and how do they act.

Refer *internal factors* in article 9.7

12. Give an account of the factors for photosynthesis. Explain the law of limiting factors in photosynthetic process.

Refer article 9.7 and 9.8

13. Enunciate Blackman's law of limiting factors. What are light and dark reactions of photosynthesis of green plants? What are 'stroma' and 'grana' and what are their functions?

For Blackman's law refer article 9.8

For light and dark reactions of photosynthesis refer article 9.4

For stroma and grana refer chapter 3, article 3.2

14. Discuss the significance of the law of limiting factors and its later modifications.

Refer article 9.8

15. Trace the path of carbon in photosynthesis.

Refer topic *fixation of CO₂ and path of carbon in photosynthesis* in article 9.4

16. What is chemosynthesis? How it differs from photosynthesis.

Refer article 9.9A.

17. What is bacterial photosynthesis? Give an account of photosynthetic bacteria clearly enumerating the ways of carbohydrate synthesis.

Refer article 9.9B

18. What is 'temperature coefficient'? Illustrate with suitable examples how knowledge of temperature coefficient helps the elucidation of the nature of physiological processes.

Refer *temperature factor* and footnote in article 9.7

19. What are dark and photochemical reactions in photosynthesis? Mention the evidences for the two processes occurring in a leaf.

Refer article 9.4 and add also *the evidences for the existence of these two phases* in the same article.

20. Discuss the relative importance of photochemical and Blackman reactions in photosynthesis.

Refer article 9.4

21. Give an account of the principal products formed in short time reduction of carbon dioxide in an algal cell in presence of light.

Refer *dark reactions* in article 9.4

22. Discuss the probable reactions involved in the reduction of carbon dioxide in presence of light.

Refer *dark reaction* in article 9.4

23. Write notes on Hill reaction.

Refer *the source of oxygen in photosynthesis* in article 9.4

24. Is there any alternate pathway for the fixation of CO₂ in photosynthesis? Cite clear evidences for the existence of this pathway.

Refer article 9.5

25. What is a Hatch and Slack pathway? Differentiate it from the Calvin-Bassham Cycle.

Refer article 9.5

26. What do you mean by C₃ and C₄ plants? Clearly explain the fixation of CO₂ in C₄ plants.

Refer article 9.5

Nitrogen Metabolism

Like carbon, hydrogen and oxygen nitrogen is also essential for the living organisms. The ultimate source of nitrogen for the autotrophic plants is undoubtedly the air. Proteins are the most important nitrogenous organic compounds found in the living organism and are essential in maintaining the structural and functional integrity of plants and animals. Most of the vital properties of the protoplasm are due to its protein composition.

Besides its importance in the properties of the protoplasm, nitrogen is essential in the synthesis of enzymes and they also enter into the chemical composition of chlorophyll and other related compounds. Nitrogen is one of the principal components of proteins and nucleic acids and thereby plays a vital role in transmission of genetic material, influencing the metabolism, growth and reproduction of the organism—plant or animal. Its role in plant metabolism is, therefore, not less important than that of carbon and other elements.

In living organisms, proteins are continuously being broken down into smaller constituents and some of these constituents (e.g. ammonia) are continuously being coupled with nitrogen to form certain compounds which are again utilized for protein synthesis. So, ammonia is considered to be the key intermediate in nitrogen metabolism and not the only compound that serves as precursor compound in the biological forms. Higher plants readily utilize inorganic nitrate ions from the soil, nitrites can also be used as nitrogen source by some of the microorganisms.

About $\frac{4}{5}$ th part of the air is composed of nitrogen and since only a limited number of organisms can use molecular or atmospheric nitrogen viz. (i) several species of blue-green algae e.g. Nostocaceae (ii) species of *Azotobacter*, *Clostridium*, *Rhizobium* etc. (iii) one species of *Rhodotorula* (iv) species of photosynthetic bacteria, there must be some way of fixing this atmospheric nitrogen within the soil. Microorganisms play an important role in fixing this atmospheric nitrogen within the soil, so that it can be utilized in the metabolic processes of higher plants. The fixation of nitrogen is, therefore, an important process where the free nitrogen of air is converted into bound nitrogen.

10.1 Source of nitrogen : The nitrogen requirements of plants are obtained from the following sources :

(a) *molecular nitrogen* or gaseous nitrogen of the atmosphere—though a limited number of organisms can utilise it directly.

(b) *nitrate nitrogen*—as nitrate ions (NO_3^-) in soil solution—is the most important source of nitrogen for the plants.

(c) *ammoniacal nitrogen*—in the form of ammonium ion (NH_4^+) and undissociated ammonia in solution.

(d) *organic nitrogen*—a large number of amino acids can be directly used as a source of organic nitrogen by plants. In fact a large number of amino acids (e.g. alanine, arginine, asparagine, glycine, histidine, glutamine etc.) have proved better nitrogen source than nitrate or ammonia (Ghose and Burris, 1950). Besides, urea ($\text{CO}(\text{NH}_2)_2$) in intact molecular form can also be used directly as nitrogen source (Webster, 1955).

10.2 A. Nitrogen fixation : Higher plants obtain nitrogen from nitrogenous compounds present in the soil. A considerable amount of nitrogenous compounds is being lost from the soil by various ways e.g. due to destruction of plant cover by different agencies like animals, fire etc. Hence to maintain a constant supply of nitrogenous compounds in the soil certain soil microorganisms known as *nitrogen fixing bacteria* play an important role. A supply of metabolic substrate like carbohydrate and in the aerobic organism a supply of oxygen are necessary for fixation of nitrogen. Regarding the specific co-factors, the role of Ca, Fe and Mo has been demonstrated, although it is not clear yet whether they participate directly in the nitrogen fixation system. The organisms which have been shown to fix nitrogen can be conveniently classified into two major groups.

(a) *Free-living forms* : Among the free living forms are certain bacteria like *Azotobacter*, *Aerobacter*, *Clostridium* and *Chromatium*, blue-green algae, for example, *Anabaena*, *Calothrix*, *Fischerella* and *Nostoc*, yeasts like *Rhodotorula* and *Pullularia* and actinomycetes like *Nocardia* can assimilate elemental nitrogen without entering into symbiosis.

(b) *Symbiotic forms* : Nodulated plants of the family Leguminosae, for example, clovers (*Trifolium* sp.), peas (*Pisum* sp.), and soyabean (*Glycine max*) in which the endophyte is a bacterium of the genus *Rhizobium*.

In certain non-leguminous root nodule-bearing plants like alder (*Alnus* sp.), *Casuarina*, *Coriaria* etc., the endophyte is usually certain actinomycetes.

Among those who have contributed much towards the understanding of mechanism of biological nitrogen fixation are Virtanen, who has mainly worked on pea nodule bacteria and Wilson and Burris, who have worked mainly with *Azotobacter*.

NITROGEN FIXATION BY FREE LIVING ORGANISMS :

I. *Blue-green algae* : The Myxophyceae or blue-green algae are without doubt extremely primitive organisms yet capable of living

photoautotrophically in an environment where combined nitrogen is lacking. They are perhaps the most promising nitrogen fixing organism so far discovered. They are world wide in their distribution (Fritsch, 1945), particularly abundant in the moist tropics. They are gregarious in their habit, forming gelatinous masses over the soil surface. Their importance in paddy fields and their role in agriculture has been worked out in India by Singh (1961) and in Japan by Watanabe (1961). Researches on physiology, bio-chemistry and nitrogen fixing capacity by these algae have been reviewed by Allen (1952 ; '56) and Fogg (1956 ; '62 ; '65).

The first concrete evidence of nitrogen fixation by blue-green algae (*Anabaena variabilis* and *Nostoc punctiforme*) came from the work of Drewes in 1928. Since then at least fourteen genera covering about forty species isolated from fresh water and other aquatic habitats have been shown to fix nitrogen.

Early workers used to grow algae in nitrogen-free medium and determined gains in combined nitrogen. Recently radio isotope ^{15}N has been widely used to demonstrate fixation by intact filaments or by cell-free extracts. The rate of nitrogen fixation of these algae is relatively slow as compared with bacterial nitrogen fixation.

It has been shown that fixation of nitrogen is restricted to the orders Nostocales (except the family Oscillatoriaceae) and the Stigonematales. A majority of soil inhabiting blue-green algae have been found in our country can fix atmospheric nitrogen (Singh, Banerjee and Singh). After isolating *Nostoc punctiforme* in pure cultures they found that these algae when freed from bacteria were unable to live in nitrogen free solution but with addition of a drop of soil extract containing soil bacteria they can thrive well. De (1939) investigated three species of *Anabaena*—*A. gelatinosa*, *A. variabilis* and *A. comulosa* var. *indica*, which have a good share in the fixation of nitrogen in the soil of rice fields of Bengal. According to him *Phormidium flaviolanum* showed no evidence of nitrogen fixation. De further observed that considerable amount of fixed nitrogen was found in the external medium in an organic form. De and Fritsch further observed that the amount of nitrogen fixed by the algae in presence of *Azotobacter* and other bacteria is the same as in pure culture.

Using radioactive ^{15}N in *Anabaena cylindrica* Cox *et al*, (1964) observed that on centrifugation highest ^{15}N -enrichment was found in fragments which comprised mainly of photosynthetic lamellae. So, it is evident that the photosynthetic activity and nitrogen-fixing activity occur in the same fraction.

It has further been found by a number of workers like Fogg (1952), Fay (1962), Stewart (1963), Venkataraman and Saxena (1963) that majority of nitrogen fixing blue-green algae liberate a considerable amount of organic form of fixed nitrogen extracellularly in the medium. The excretion of different organic forms of nitrogen like

amides, peptides and free amino acids have been observed by many. Thus using ^{15}N in nitrogen fixing algae *Westelliopsis prolifica* (Stigonemataceae) Pallnaik (1964) observed that the nitrogen liberated in the medium appeared in the form of ammonia whereas amides are liberated afterwards. This finding clearly indicates that ammonia is the key intermediate in nitrogen fixation. Similar conclusion has also been obtained from the studies of *Clostridium* and *Azotobacter*. Extracellular evidence of amino acids and peptides although not directly related with the fixation process but are extremely important as other organisms can utilize them without cell autolysis.

Since majority of paddy fields of south-east Asia are covered by profuse growth of many nitrogen fixing algae, they therefore contribute much of the fixed nitrogen for the rice plants in many tropical soils. The possibility of using these algae as green manure opened up a new possibility in increasing the yield of paddy in Japan. Nitrogen fixing blue-green algae are also equally important in relation to soil fertility in the desert area (Shields and Durrell, 1964). It has also been observed that some of the heterotrophically growing algae like *Nostoc* in certain depth of sea or in lakes can also fix nitrogen. In addition, many other species like *Anabaena*, *Gloeotrichia*, *Nodularia* and *Anabaenopsis* probably do likewise.

II. *Bacteria*: The first evidence that microorganisms can fix molecular nitrogen came from the work of Jodin in 1862. Then in 1885, Berthelot working along similar lines came to the same conclusion. But it was after eight years, Winogradsky (1893) first isolated from soil the anaerobic organism *Clostridium pastorianum* (now *C. pasteurianum*). In 1901 Beijerinck discovered another group of aerobes *Azotobacter chroococcum* and *A. agilis* all of which are capable of fixing molecular nitrogen. For nearly half a century the main work of nitrogen fixation is centred round the physiology of these two genera. Photosynthetic bacteria like *Rhodospirillum rubrum* are found to fix nitrogen (Kamen and Gest, 1949). Up-to-date eighteen different bacterial genera have been found able to fix molecular nitrogen.

Many genera of the family Azotobacteraceae (e.g. *Azotobacter*, *Beijerinckia* and *Derxia*) can fix molecular nitrogen. These are gram-negative, aerobic heterotrophic rod like bacteria. The most important genus among these is *Azotobacter* which has world wide distribution. Amongst three species of *Azotobacter* (e.g. *A. chroococcum*, *A. agilis* and *A. vinelandii*) considerable work has been done on *A. vinelandii* and is said to be the most important nitrogen fixing organism. This bacteria fixes nitrogen in a slight alkaline medium and requires an optimum temperature of 25-28°C.

In 1950, Drex created a new genus *Beijerinckia* (Syn. *Azotobacter indicum*, isolated from Indian rice fields) for its marked difference in morphological and physiological characters. Although this genus is widespread in tropical and lateritic soils, much more research has still to be done on its nitrogen fixation.

The genus *Derxia* has got one species *D. gummosa* which is another gram-negative, aerobic bacteria has been isolated from the soils of West Bengal (Jensen *et al*, 1960). It is another efficient nitrogen fixing organism which can fix molecular nitrogen at a wide pH range (5.0-9.0) and temperature (15-42°C).

The most important anaerobic bacteria that can fix nitrogen is *Clostridium*. This is a gram-positive, rod like bacteria. The important species is *Clostridium pasteurianum*, which has contributed much to our understanding of the nitrogen fixation. The optimum temperature for nitrogen fixation is about 25°C for this bacterium.

Besides these, there are three families of photosynthetic bacteria (e.g. Chlorobacteriaceae, Thiiorhodaceae and Athiorhodaceae) which contribute much in the nitrogen fixation. Among Chlorobacteriaceae *Chlorobium* is a non-motile, gram-negative, rod or oval-shaped anaerobic organism. This can fix nitrogen in presence of light. Among Thiiorhodaceae, *Chromatium* is a motile, oval, light dependent nitrogen fixing organism. Several genera of the family Athiorhodaceae : *Rhodospirillum*, *Rhodopseudomonas* and *Rhodomicrobium* can also fix nitrogen. They also fix in an anaerobic condition in presence of light.

A large number of other nitrogen fixing bacteria e.g. *Pseudomonas* and *Achromobacter* has been demonstrated by Proctor and Wilson (1955). Among *Pseudomonas* six gram-negative, motile, rod like strains has been demonstrated, all of which fix nitrogen under aerobic or anaerobic conditions; whereas the eight strains of *Achromobacter* fix nitrogen anaerobically. Other nitrogen fixing gram-negative, rod like anaerobic organisms are *Aerobacter*, *Bacillus*, *Spirillum*, *Methanobacterium*. The detailed work on nitrogen fixation by these bacteria have been carried out.

SYMBIOTIC NITROGEN FIXATION :

I. *Legume* : The pioneer workers on this subject were Hellriegel and Wilfarth (1888) who first showed that so long as the nodules were present leguminous plants were able to increase the nitrogen content even when there were no nitrate or ammonium salts in the soil. They therefore suggested a relationship between the nodule bacteria and the host plant to be a case of 'symbiosis'—where both the partners were mutually benefited as a result of their association. This symbiotic bacteria at that time was known as *Bacillus radiculicola* (Beijerinck, 1888), which has been renamed latter on as *Rhizobium leguminosarum* (Frank, 1890).

Symbiotic nitrogen fixation is mainly carried out by the activities of *Rhizobium* species. These are gram-negative, rod shaped in structure which enter through the root hairs of leguminous plants and form characteristic nodules. The sequence of events in the development of nodules is extremely complex. The exact nature of stimulatory material which first attract the bacteria is still uncertain, but according to West and Wilson (1940) biotin may be an important stimulatory

material. Amino acids, enzymes, sugars and vitamins may be other possibilities. It has also been shown that the secretions produced by a legume, stimulate multiplication of *Rhizobium* strains. The bacteria then secrete certain growth substances like indole acetic acid (IAA) which causes many of the root hairs to curl. When the root hairs are infected with bacteria, the bacteria move towards the cell in the form of a non-septate thread like structure known as *infection thread*. At this stage the bacteria are still normal in their structure and characteristics. But then they increase in size and assume a diversity of shapes and stop dividing, these are then called *bacteroids*. Bacteroids occupy a larger volume as compared with its original *Rhizobium* cell and thus there is an increase in the size of the infected cells. Further development of nodule depends on the genetic constitution of the host plant. As the host plant contains tetraploid cells in addition to its normal diploid cell in the root cortex and when this infection thread comes in contact with tetraploid cells, it apparently stimulates the surrounding cells to meristematic activity and thus results in the formation of a *nodule*.

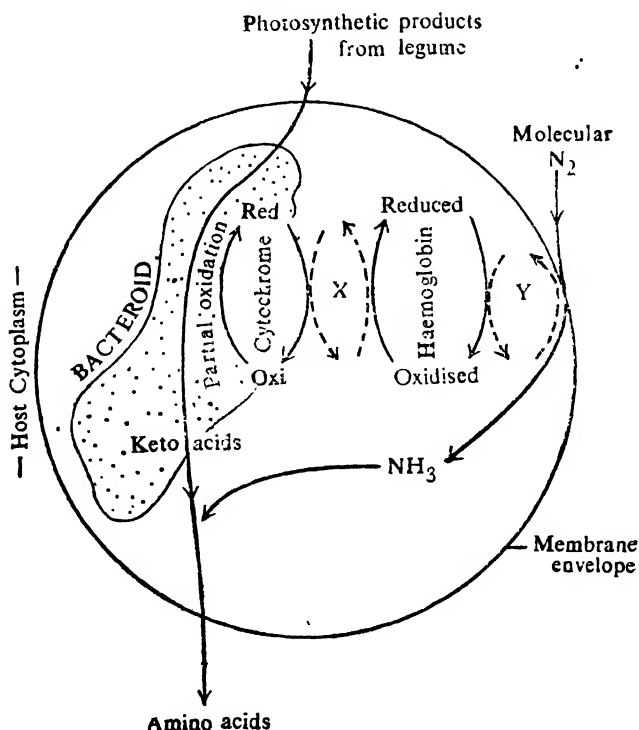


Fig. 10.1 Diagram showing the sequence of reactions in nitrogen fixation by legume root nodules. X and Y represent the unknown link of electron transport.

The steps in nitrogen fixation by this nodule bacteria have been worked out by Bergersen and Wilson (1959 ; '60). With the help of radioactive ^{15}N they concluded that the site of fixation appears to be associated with the host plant membrane.

According to Bergersen (1960) haemoglobin acts as an electron carrier. The reducing power generated in the bacteroids is transferred the nitrogen fixing membrane via cytochrome and haemoglobin. Under anaerobic condition the molecular nitrogen can oxidise haemoglobin which will be again reduced by the bacteroids and thus molecular nitrogen will be converted to ammonia (NH_3). The bacteroids receive the photosynthetic products from the host plant and which serve as a source of reducing power. The keto acid formed due to partial oxidation of the photosynthetic products unite with ammonia to give rise to amino acids. Bergersen's hypothesis is represented in Fig. 10.1.

II. *Non-legumes* : Fixation of nitrogen is not only restricted to the nodulated leguminosae, but there is a group of non-leguminous angiosperms, which produce nodules and can fix nitrogen as efficiently as those of legumes. The most important non-leguminous genera are *Alnus*, *Casuarina*, *Coriaria*, *Myrica* etc. which are all woody perennials and bear nodules inhabited by certain filamentous bacteria (actinomycetes).

The possibility of nitrogen fixation by the nodulated non-legumes came from the work of Nobbe *et al* in 1892 and then in 1904 by Hiltner. The nitrogen fixation by these plant has been confirmed unequivocally by a number of subsequent workers. The formation of nodules by these plants follow almost the same principle as in the legumes.

B. Biochemistry of nitrogen fixation : From the biochemical view point nitrogen-fixing and non-nitrogen-fixing organisms are similar except the former have in addition a number of enzymes by

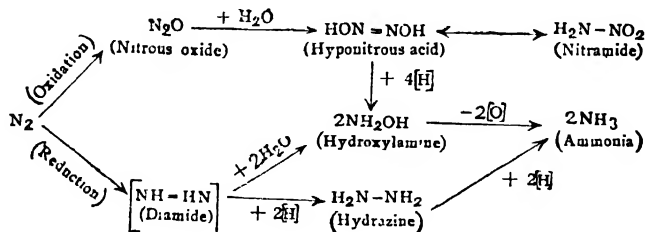
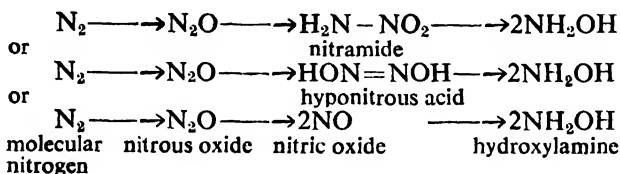


Fig. 10.2 Possible biochemical pathways of nitrogen fixation.

which they fix molecular nitrogen from the atmosphere. Biochemical studies indicate that both in *Azotobacter* and *Clostridium* ammonia is the key intermediate in nitrogen fixation (Burris and Wilson, 1957). Although the exact biochemical changes in conversion of nitrogen

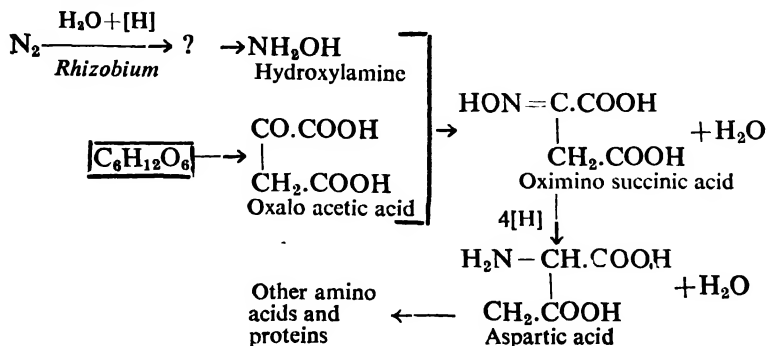
to ammonia are not known but the possible intermediate steps may be shown schematically in the previous diagram.

It is evident that the molecular nitrogen enters combination either by oxidation or reduction. If the initial step were oxidative, the first product of this oxidation is nitrous oxide (N_2O) or some other related compounds like hyponitrous acid ($HON=NOH$) or nitramide (H_2N-NO_2). Among the intermediates, nitramide although decomposes rapidly in solution and hyponitrous acid is a general poison, does not mean that they are not intermediates. Recently (Fewson and Nicholas, 1960) it has been found that in *Anabaena* nitric oxide (NO) may be an intermediate in this oxidative pathway. Whatever may be the possible intermediate products, hydroxylamine (NH_2OH) has been considered to be the end product before its ultimate conversion to ammonia. So considering all the above possibilities the conversion of nitrogen to hydroxylamine can be summarized as



Recent work of Bulen *et al*, (1964) clearly suggests that the oxidative step is unnecessary and the reductive pathway is more likely. In the reductive pathway diamide ($NH=HN$) or hydrazine (H_2N-NH_2) is the possible intermediate before ultimate conversion to ammonia. Among the reductive intermediates, hydrazine is found to be the more possible compound as it has been based on recent findings. Further, diamide is found to be extremely labile.

Vitranen *et al*, (1947) showed that in legume roots the key intermediate in nitrogen fixation is hydroxylamine which reacts with oxaloacetic acid to give rise to oximino succinic acid. This oxime is further reduced to aspartic acid according to the following scheme.



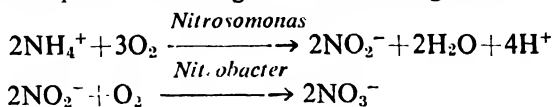
The presence of hydroxylamine reductase in legume nodule and *Anabaena cylindrica* clearly suggests that hydroxylamine is a common intermediate in nitrogen fixation (Hattori, 1962).

It is evident from the above discussion that whatever may be the hypothetical pathway for nitrogen fixation in different groups of nitrogen fixing organisms, three major components are necessary; a source of reducing power, an energy source and appropriate enzyme systems.

Regarding the source of reducing power it is evident that pyruvic acid, molecular hydrogen or direct photoreduction are the main sources, of reducing power. Regarding the requirement of energy, it has been proved definitely that ATP is essential for nitrogen fixation in some of the nitrogen fixing organisms (e.g. *Azotobacter*, *Rhodospirillum rubrum*). The two main enzymes in nitrogen fixation are *nitrogenase* and *hydrogenase*. Nitrogenase is mainly responsible for reduction of molecular nitrogen. Although this enzyme remains in the plant, but very little is known about its properties and activities. The hydrogenase is responsible for the conversion of hydrogen ions to molecular hydrogen and has been detected in all nitrogen fixing organisms. Like nitrogenase, the nature of hydrogenase is still uncertain.

10.3 Absorption of nitrogenous compounds from the soil :

There is little evidence that the plants can utilize atmospheric nitrogen to synthesize the complex nitrogenous compounds. But majority of the land plants get their nitrogen from the different forms of nitrogenous compounds present in the soil viz., (i) nitrates, (ii) nitrites, (iii) organic nitrogenous compounds and (iv) ammonium salts. Soil nitrate represents the principal source of nitrogen for higher plants and the accumulation of nitrate in soil is continuously taking place due to microbial oxidation of ammonia. The microbes which are essential for the conversion of ammonium salts to nitrate have been isolated first by Winogradsky (1890). These are *Nitrosomonas*—converting ammonium ions (NH_4^+) to nitrite (NO_2^-) and *Nitrobacter*—which further oxidise nitrite (NO_2^-) to nitrate (NO_3^-). The conversion takes place according to the following scheme.



The conversion of ammonia to nitrate by *Nitrosomonas* may involve hydroxylamine as an intermediate but very little is known about the other possible intermediates (hyponitrite, nitramide etc.) in the above conversion. The oxidation of nitrate to nitrite by *Nitrobacter* has not been studied extensively, but has been found to involve the cytochrome system.

Absorption of nitrate by plants takes place through ionic exchange mechanism in the roots and which is then reduced to other forms

as soon as it enters the plant body. Plants can also absorb nitrites directly as a source of nitrogen. In some cases ammonium salts that are in a reduced state may be utilized by the plants as a direct source of nitrogen.

10.4 Reduction of nitrate in plant tissues : The first step in the utilization of nitrate (NO_3^-) by the plant is its reduction to nitrite (NO_2^-). The process is catalyzed by the enzyme *nitrate reductase* which is found widely in higher plants.

Nitrates that are absorbed by roots are gradually reduced or stored up for a considerable period within the tissues. One mechanism takes place in the roots or other non-green parts while another takes place within leaves or green parts of the plants. In the former case, the energy required for nitrate reduction is derived from the oxidation of carbohydrates in respiration. Nitrate is reduced to nitrite which appears at the intermediate stage. According to Chibnall, nitrates are further reduced to ammonia through a series of intermediate stages like hydroxylamine, hyponitrous acid etc. Ammonia is then utilised in the formation of amino acids or other related compounds. The pathway of this process is diagrammatically represented in Fig. 10.3.

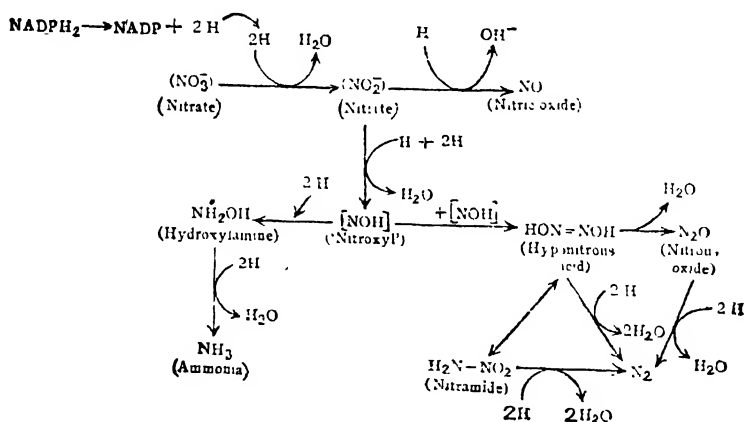


Fig. 10.3 Pathway of reduction of nitrate to ammonia, nitric oxide, nitrous oxide and nitrogen in higher plants and microorganisms.

The reduction of nitrate is catalyzed by the enzyme *nitrate reductase*. Nitrate reductase is a metalloflavoprotein enzyme. It includes a reduced pyridine nucleotide (NADP^+ or NADPH) as an electron donor, flavin adenine dinucleotide (FAD) as a prosthetic group and molybdenum (Mo) as a co-factor. In this system electrons are passed from reduced pyridine nucleotide to flavin adenine dinucleotide converting it to reduced FAD (FADH_2). According to Nicholas and Nason (1954) the electrons from FADH_2 is then transferred to oxidised molybdenum resulting in reduced molybdenum.

Reduced molybdenum then passes electrons to nitrate converting it to nitrite

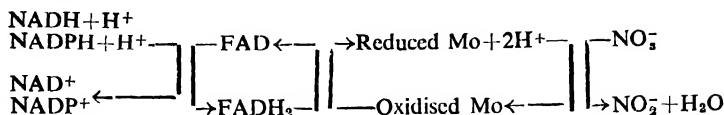
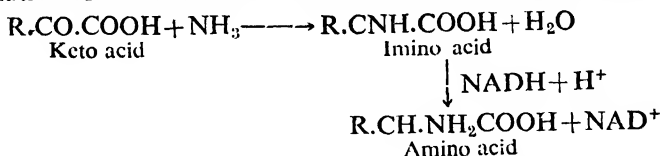


Fig. 10.4 The sequence of electron transport system in the nitrate reduction catalysed by the enzyme nitrate reductase.

In case of leaves light plays an important role in the nitrate reduction process. According to Burstrom light acts as a source of energy and the process is related with the carbon dioxide reduction during the process of photosynthesis. It is believed that in the leaves, nitrate is reduced to some intermediate compounds which combine with an intermediate product of photosynthesis giving rise to amino acids or other nitrogenous organic compounds. In this process light energy is utilised instead of respiratory energy.

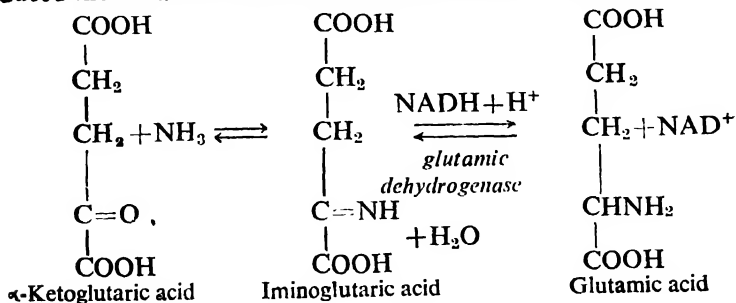
10.5 Synthesis of amino acids : Amino acids are compounds having the properties of both amines and acids. Each amino acid consists of at least one carboxyl ($-\text{COOH}$) group and one or several amino ($-\text{NH}_2$) group. There are two main processes by which majority of amino acids in plants are found to be synthesized.

(i) *Reductive amination*—The general principle of this process is the formation of amino acids from an keto acid reacting with ammonia.



So amino acids are synthesized in two steps—the union of ammonia with a keto acid to form imino acid which is subsequently reduced to amino acid.

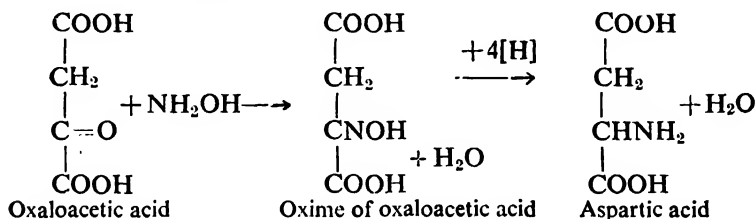
The first step proceeds spontaneously, but the second reaction is catalysed by the dehydrogenase enzyme and requires the presence of reduced nicotinamide adenine dinucleotide ($\text{NADH} + \text{H}^+$).



This reaction is catalysed by the enzyme *glutamic dehydrogenase* with coenzyme NAD^+ .

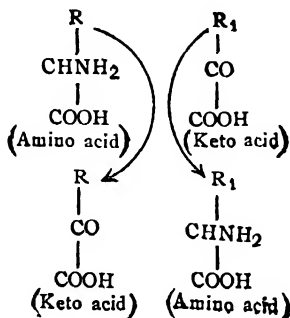
Aspartic acid and alanine are the other amino acids which may arise from oxaloacetic acid and pyruvic acid in similar way. Amino acid synthesis through this process is closely related to the process of aerobic respiration and organic acid metabolism. During aerobic oxidation of pyruvic acid the conversion of α -ketoglutaric acid to glutamic acid, oxaloacetic acid to aspartic acid and pyruvic acid to alanine is considered as side reactions of Krebs cycle.

Amino acid synthesis may also take place when a keto acid reacts with hydroxylamine. This intermediate stage is known as oxime of that particular keto acid.



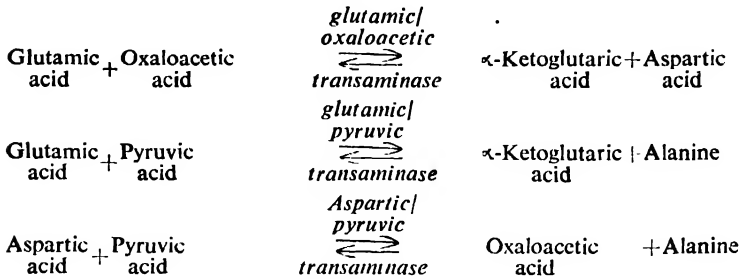
This type of reaction is only applicable to plants which have a symbiotic association and is not found in other plants.

(ii) *Transamination*—It involves the transfer of amino group from one amino acid to the carboxyl group of a keto acid without the intermediate formation of free ammonia. It has been suggested that glutamic acid is the main amino acid from which other amino acids are formed through transamination. As soon as the inorganic nitrogen enters through the amination system with α -ketoglutaric acid to form glutamic acid, it is available for the synthesis of other plant amino acids by transamination system.



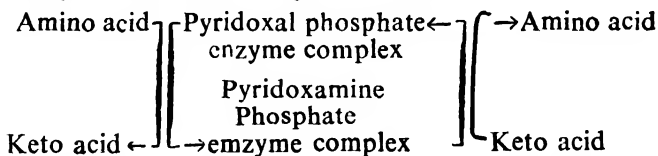
The enzyme responsible for such reaction is termed as *transaminase* and the name of the specific *transaminase* is given to the specific substrate on which it reacts.

A typical transamination was first observed by Herbst and Engel (1934). Subsequent work of Cohen (1943) also suggests the existence of transamination system, which occurs as follows :



Transaminase enzymes of varying degrees of specificity are found to catalyze the above reactions.

It has been found by Braunstein and Kritzmann (1937) that transamination is accomplished by a condensation of amino acid and keto acid to form a labile intermediate, which then undergoes rearrangement and hydrolysis. It has further been experimentally proved by Peterson *et al*, (1954) that the transaminase enzyme has a prosthetic group (co-factor) known as pyridoxal phosphate (a derivative of vitamin B₆—pyridoxine), which accepts amino group of the amino acid of the reacting system and itself being converted to pyridoxamine phosphate. According to this hypothesis the pyridoxamine phosphate then donates this amino group to another keto acid converting it to corresponding amino acid.



Majority of the amino acids in plants are found to be synthesized by this process.

Besides these, there are several amino acids present in plant cells which are formed from the hydrolysis of protein or from chemical transformation of acid amides.

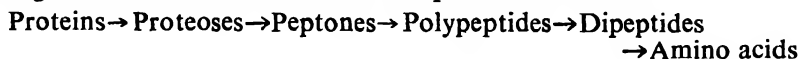
10.6 Protein synthesis: Proteins are complex organic compounds formed by the condensation of amino acids. All proteins contain carbon, hydrogen, nitrogen and oxygen. In some cases sulphur and phosphorus are also present.

The various theories put forward to explain the mechanism of protein synthesis may be broadly classified into two groups.

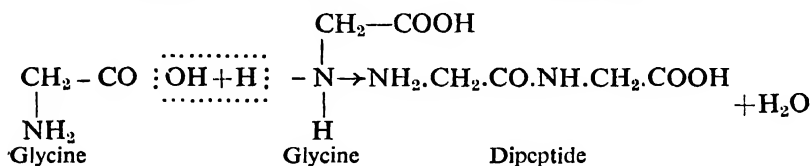
(A) polypeptide linkage hypothesis and (B) template hypothesis.

(A) *Polypeptide linkage hypothesis*—It is one of the earliest theories regarding protein synthesis which substantiates that it took

place by the reverse of protein hydrolysis or degradation. On complete hydrolysis proteins always give amino acids as end products through a number of intermediate compounds as follows :

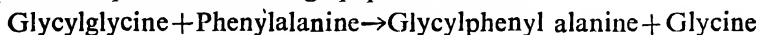


Emil Fischer was the first to suggest the formation of proteins by the condensation of amino acid molecules. He linked amino acid molecules by *peptide linkage* and thus produced a synthetic polypeptide. A peptide linkage is that in which amino group of one amino acid molecule is bound with a carboxyl group of another amino acid molecule ; one molecule of water is liberated during the process. Formation of dipeptide by the condensation of two amino acid molecules (e.g. glycine) takes place in the following way.



The dipeptide formed from the condensation of two amino acid molecules also possesses one carboxyl group and one amino group to which other amino acids can be joined or linked. In this way series of amino acid molecules can be linked or added by peptide linkage. According to this view at first polypeptides, peptones, proteoses and then proteins are formed by the polymerisation or condensation of more and more amino acid molecules.

This theory also involves the formation of proteins by the process of transpeptidation (Bergman and Fruton) or transamidation (Waelsch *et al*). Transpeptidation involves increase of one peptide with decrease of another by the proteolytic enzymes releasing the amino acids. This amino acid is then transferred to another amino acid or peptide acceptor to form large peptide. Thus.



The main drawbacks of this theory are :

(i) this mechanism requires the presence of peptides and polypeptides as intermediates. But occurrence of sufficient quantities of peptides has not been proved.

(ii) it can not explain the sequence of amino acids in the newly synthesized protein molecule.

(iii) it involves a series of enzymes in the synthesis of a single protein and synthesis of different proteins needs "an infinitely receding series of enzymes which are inevitably an impossible concept."

(B) *Template hypothesis*—There are certain protein molecules that can duplicate themselves within the living cell from time to time ;

this suggests that the pre-existing protein molecule serves as a *template* or *model* upon which other molecules of some protein are constructed.

Dounce (1952) based his theory on :

(a) implication of polynucleotides in determining the sequence of amino acids in proteins ;

(b) activation of nucleic acid by the formation of triple esterified phosphate ;

(c) activation of amino acids initially through their amino group.

Borsook (1956) further elaborated by suggesting that amino acids are attached to nucleic acids by their carboxyl group.

According to Hoagland (1958) the mechanism of protein synthesis involves three steps.

(i) activation of amino acids in the presence of ATP and specific activating enzyme to form "amino-acyl AMP."

(ii) incorporation of the activated amino acids into soluble RNA. This soluble RNA acts as a template on which amino acids attach closely.

(iii) incorporation of the soluble RNA and amino acid into RNA of microsomes. This microsomal RNA has been termed "secondary template" by Hoagland.

There is another hypothesis known as *keto peptide hypothesis*. According to this, condensation of keto aldehydes or keto acids with amino acids produces keto peptides, which by transamination and further polymerisation or condensation process give rise to protein (Virtanen, 1950).

Role of nucleic acid in protein synthesis—The most characteristic feature of protein is that they are unique to the particular species or individual i.e. they are highly specific. This specificity of protein is due to the sequence in which the amino acids are present in the protein. Any theory of protein synthesis should therefore include an explanation by which the amino acids come to occupy their respective positions in the protein.

Most up-to-date knowledge of protein synthesis is based mainly from the experiments of Hoagland (1958).

The modern theories involve the action of RNA molecules, which act as templates for protein synthesis and they are found to be effective only when attached to the ribosomes.

The central dogma in protein synthesis is as follow :

$$\text{DNA} \xleftarrow{\text{replication}} \text{DNA} \xrightarrow{\text{transcription}} \text{RNA} \xrightarrow{\text{translation}} \text{Protein}$$

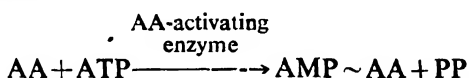
Using a number of different techniques including the use of radioactive isotopes it is possible to trace the main steps of protein synthesis in plants.

The gene in the nucleus i.e. a portion of DNA molecule controls the synthesis of specific RNA molecule which is complementary to the DNA, the genetic message may therefore be transferred to the site of protein synthesis. RNA is thus a reverse copy of its DNA template. This RNA is known as *messenger RNA* which passes into the cytoplasm and becomes associated with the ribosomes, which incidentally form a peculiar configuration on its wall layer and which itself now becomes a template for protein synthesis (Fig. 10.5).

The other RNA already present in the cytoplasm pick up the individual amino acids and carry them near the ribosomes. Those RNA that carry amino acids are known as *transfer RNA*. This transfer RNA with amino acid then moves and assumes position on the RNA of the ribosomes in a definite sequence. The order of this arrangement is however determined by the surface pattern of the RNA molecules of the ribosomes. Bonds are then formed between the adjacent amino acids and the attached amino acids fall off the transfer RNA, thus a new polypeptide chain, a part of the protein molecule is synthesized. The transfer RNA is thus freed to be available again for picking up another amino acid.

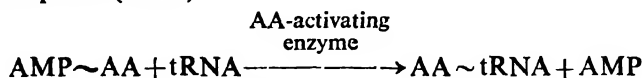
It is evident from all the above findings that the whole process of protein synthesis may be divided into three steps :

(a) *Activation of amino acids* : The first step of protein synthesis involves activation of amino acid. Selection of amino acids from the heterogenous pool in the cytoplasm is highly specific and is accomplished by the specific activating enzyme. In the formation of this 'active' compound the energy is derived from breaking of pyrophosphate bond of ATP.



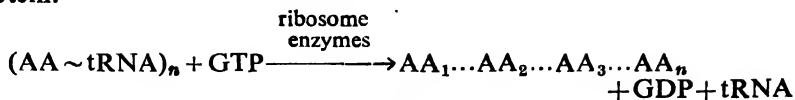
The products are the activated amino acid (AMP ~ AA), known as amino acyl adenylate and pyrophosphate (PP).

(b) *Amino acid-tRNA complex* : This activated amino acid now combines with the specific type of RNA. This RNA is referred to as *soluble RNA* (sRNA) or *transfer RNA* (tRNA) or *adapter RNA*. Actually before the attachment of activated amino acid with this RNA, there is a preparation of an acceptor site usually by reacting with cytidine triphosphate (CTP) and adenosine triphosphate (ATP). The AMP ~ AA complex is now attached to the phosphorylated tRNA to produce an amino acid-tRNA complex and adenosine monophosphate (AMP).



(c) *Polypeptide formation* : This reaction takes place on the surface of ribosomes. Here the amino acid is released from the tRNA by guanosine triphosphate (GTP) in presence of specific enzyme

of ribosome and is incorporated into a polypeptide chain to form a protein.



As a result of this reaction tRNA and guanosine diphosphate (GDP) are released.

The synthesis of protein chain starts at the amino end of the polypeptide and proceeds to the carboxyl end. Thus

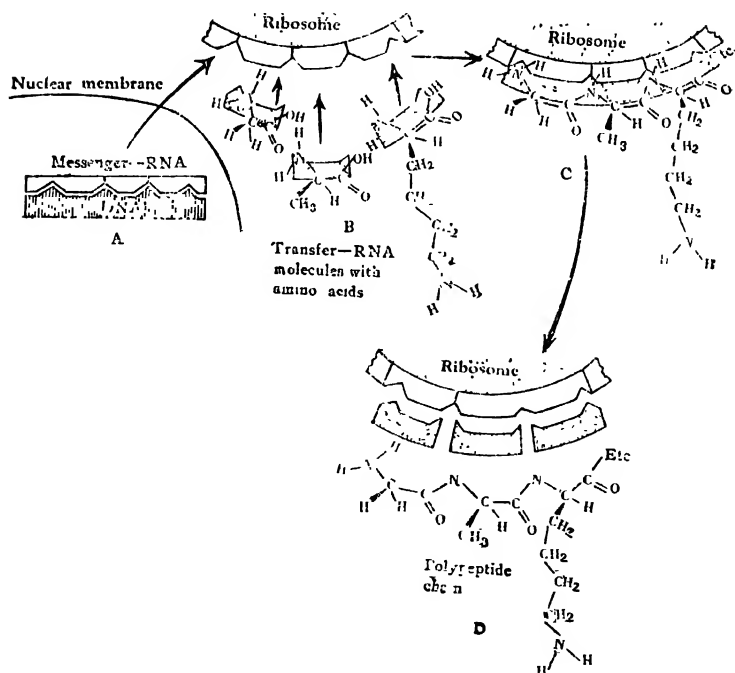
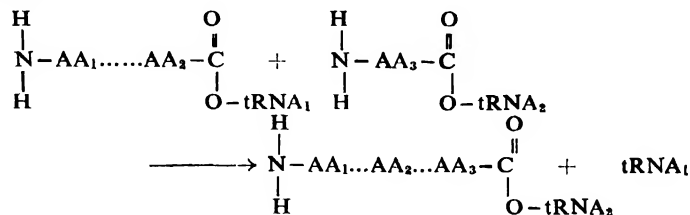


Fig. 10.5 A diagrammatic representation of the synthesis of a chain structure (polypeptide chain) from three amino acids.

The whole idea of messenger RNA and its functioning in the synthesis of protein was suggested by Jacob and Monod (1961). So,

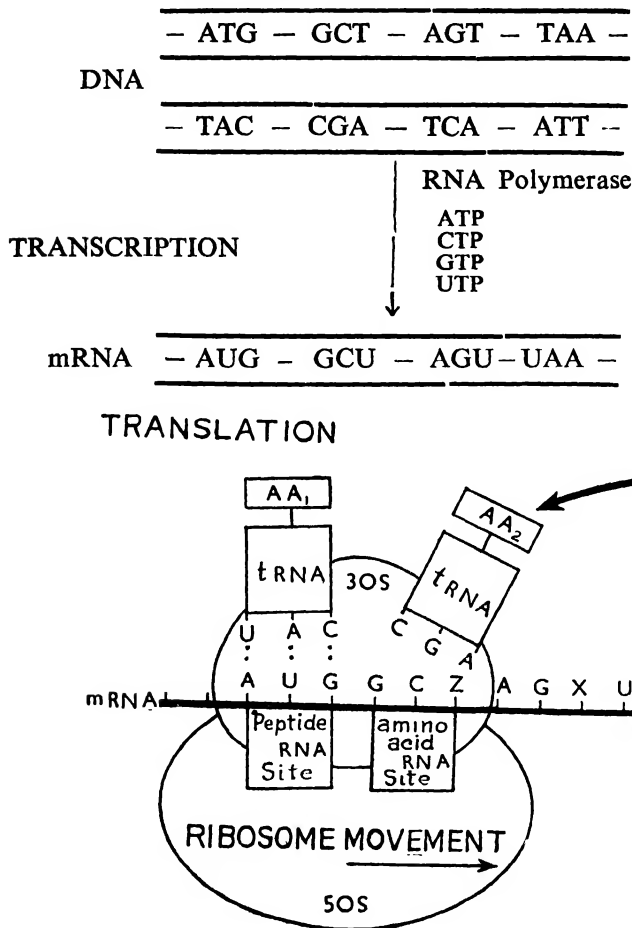


Fig. 10'6 Diagram illustrating a possible scheme of protein synthesis.

Transcription: The mRNA molecule formed is complementary to one strand of the DNA template. The bases in the mRNA are the same as in DNA except thymine is replaced by uracil in mRNA. The genetic message encoded in mRNA is then carried from the nucleus and joins the 30S component of ribosome.

Translation: The first amino acid (**AA₁**) of the protein chain locates on the peptide-tRNA site. The amino acid-tRNA site is activated to receive the incoming second amino acid (**AA₂**). **AA₁**=formylated methionine; **AA₂**=alanine. **AUG**=codon for formyl methionine when in front position on mRNA. **GCU**=Codon for alanine, where **Z** can be U, C, A or G, here **Z** is taken as U for binding with the anticodon **CGA**; **X**=either base U or C, here **X** is U for anticodon binding; **UAA**=codon for chain termination.

according to them the DNA transfers genetic information to newly formed RNA (mRNA) which carry the coded information to the site of protein synthesis (ribosomal surface). So mRNA acts as a template to aggregate amino acyl-tRNA molecules in the proper order to allow the synthesis of peptide chain with the proper sequence of amino acids. The peptide bonding between successive amino acids takes place by a 'zipper action,' where the new amino acid molecules are added to the growing chain. Usually two such amino acids unite at the rate of about two a second and a protein molecule, of approximately 150 amino acids is formed in 1.5 minutes. In microorganisms, however, a few seconds are sufficient for protein synthesis. After their synthesis the proteins are separated out from the template on the ribosomes. It has been observed by a number of scientists that probably the condensing and releasing enzymes are also required in the protein synthesis although very little is known about these at present.

A schematic representation of the proposed mechanism is given in Fig. 10.5.

The chain elongation by amino acid polymerization in which the amino acids are joined together to form peptide bonds involves two enzymes and GTP in the cytoplasm. *Transferase I* kicks off the AA_1 (Fig. 10.6) to the amino acid-tRNA site attach it to the AA_2 by a peptide bond. The peptide-tRNA side is opened by this action. The *transferase II* helps to translocate the tRNA - AA_2 - AA_1 from amino acid-tRNA site to peptide-tRNA site. Associated with the enzymatic activity the movement between the ribosome and mRNA helps the next codon triplet to move into the new position. This translocating activity thus opens the amino acid-tRNA site for the third amino acid (AA_3) coming in as tRNA - AA_3 . A repetitive continues for chain elongation and as the cycle is repeated, the polypeptide chain is elongated, one amino acid at a time. The nonsense codons UAA, UAG and UGA serve as terminator signals.

The concept of protein synthesis outlined above in many of its features is still very speculative. Many more details are yet to be learnt to correlate the steps in a proper way to reject the speculation or substantiate it.

10.7 Nitrogen cycle: Nitrogen though an inert gas is very important as it is the main constituent of protein. Hence it plays an important role in the protein metabolism of plants as well as of animals. Atmospheric air is the vast natural source of free nitrogen, which indirectly or directly is utilized in protein metabolism and again by death and decay of living organisms, nitrogen goes back to the air—these complete series of events which occur partly in micro-organisms of the soil and partly in the tissues of higher plants are collectively known as *nitrogen cycle*.

The nitrogen cycle involves several processes. First, we begin with the dead plants and animals, the nitrogen compounds, mainly

the protein present in all of them pass into the soil. Many of the soil microorganisms then decompose protein with the liberation of a number of simpler substances, one of which is ammonia (NH_3). In the upper layer of the soil where the decomposition of proteins is taking place, there are many side reactions which involve the formation of certain acids in the soil. The soil water therefore contains a number of hydrogen ions (H^+) which chemically unite with the free ammonia to form ammonium ions (NH_4^+). These ammonium ions can be directly absorbed by some plants which synthesize their protein, thus completing a short nitrogen cycle.

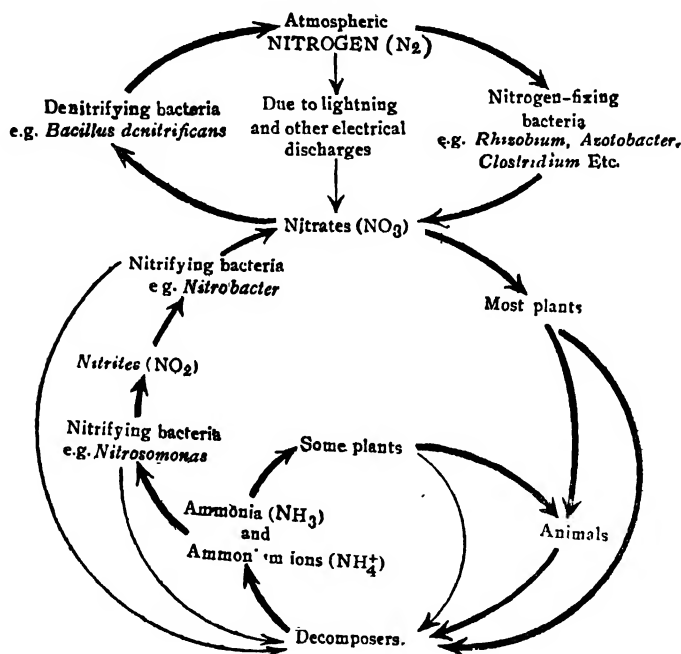
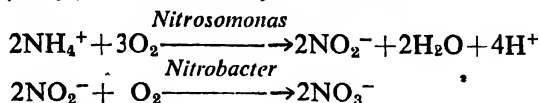


Fig. 10.7 Nitrogen cycle.

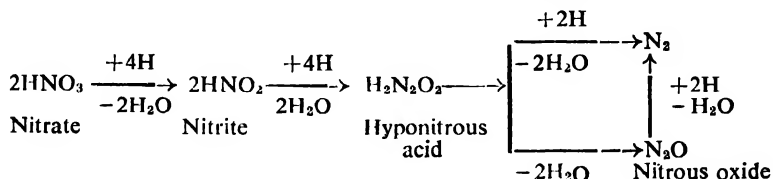
The main pathway of ammonium ions, however, takes place in the following way. The ammonium ions are oxidised by a group of bacteria in the soil known as *nitrifying bacteria* or *nitrobacteria*. One of these bacteria is *Nitrosomonas* which convert ammonium ions (NH_4^+) into nitrite ions (NO_2^-); further oxidation of nitrite into nitrate ions (NO_3^-) is continued by *Nitrobacter*.



Recently, it has been observed that nitrification may also be brought about by certain heterotrophic soil fungi e.g. strains of

Aspergillus flavus and some species of *Penicillium*. In general, majority of the land plants utilize nitrate and build their necessary protein and this closes the second nitrogen cycle.

The nitrifying bacteria usually live under aerobic condition and can therefore utilize oxygen from the atmosphere. Under anaerobic condition the nitrifying bacteria can not carry on their activities, naturally there is an accumulation of large amount of nitrogen containing compounds—which are mostly unavailable to the plants. The denitrifying bacteria then convert part of these nitrates to molecular nitrogen gas which escapes to the atmosphere. The conversion takes place according to the following scheme.



The organisms responsible for denitrification are *Bacillus denitrificans* and the species of *Pseudomonas*, *Micrococcus* etc. Several autotrophs like *Thiobacillus denitrificans*, *T. thioparus* are also capable of reducing nitrates.

So by this process there is a possibility of gradual increase in the nitrogen content of the atmosphere. But in practice, however, this does not happen as the nitrogen content of the atmosphere (about 78%) has remained practically constant. So there must be some way of reconvertng a part of the atmospheric nitrogen to nitrogenous compounds and lightning may change a small amount of atmospheric nitrogen to nitrogenous compounds. But the major process in the biosphere is the action of *nitrogen fixing organisms* which can fix a major part of atmospheric nitrogen to nitrate (NO_3^-) (refer article 10.2) and thus a balance is actually maintained between the atmospheric nitrogen and the nitrogen content of the soil through this cycle.

10.8 Experiments on nitrogen metabolism :

(i) *Utilization of nitrates by green plants*—A well grown potted plant was taken and some 50 ml of 0.001M solution of $\text{Ca}(\text{NO}_3)_2$ was poured on the soil. The whole set was then kept in a dark chamber for 3-4 days. After that the pot was removed to light and immediately some sections were cut from the petioles of the leaves. The section was the examined in a drop of diphenylamine sulphate reagent.¹ The blue colour in the section indicates the presence of nitrates.

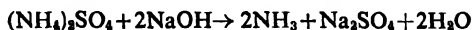
After several hours similar test was made to find out the presence of nitrate in the petiole and it was then compared with the previous section for the quantity of nitrate present.

¹ Dissolve 0.03 g of diphenylamine in 25 ml of pure sulphuric acid free from nitrate to give rise to diphenylamine sulphate reagent.

(ii) *Estimation of total nitrogen by Kjeldahl's method*—The method of estimation is based upon the fact that most nitrogenous substances are quickly decomposed to ammonium sulphate on heating with conc. H_2SO_4 .



When the decomposition products are distilled with excess NaOH ; ammonia is liberated.



The liberated ammonia is absorbed by a known volume of standard acid and the amount of ammonia is determined by titration.

20-30 mg of dry powdered material (amount may vary according to the anticipated amount of nitrogen) was taken in Kjeldahl's digestion flask, to it small quantity of reduced iron was added. Then 4 ml of distilled water and 1 ml of 50% H_2SO_4 was poured carefully washing the flasks. The flask was then heated for 30 minutes over a small flame until the volume is reduced.

After cooling, 2 ml of nitrogen-free H_2SO_4 (conc.) and small amount of potassium sulphate and copper sulphate (1 : 3) was added in the flask. Then digest the material until the solution is colourless.

The cooled digested material was then transferred to Kjeldahl's distillation apparatus and excess of 40% NaOH is added. The other end of the distillation apparatus dips in a conical flask containing 10 ml of $\text{N}/100$ HCl with a drop of Weslow's indicator to absorb the ammonia liberated during distillation. The excess acid was then titrated with $\text{N}/100$ NaOH .

A blank experiment was performed under identical condition and thus from the difference between these two experiments, the amount of nitrogen present in the plant material can be calculated by the following formula.

$0.00014 \text{ g} \times \text{N}/100 \text{ HCl consumed} \times \text{factor of N}/10 \text{ HCl} = \text{g of nitrogen in the material.}$

SELECTED QUESTIONS

1. What are the chief sources of nitrogen for the higher plants?

Refer article 10.1

2. Discuss in the light of recent researches the chemical reactions involved in the biological nitrogen fixation.

Refer article 10.2

3. Give a brief account of nitrogen fixation by free living bacteria and blue-green algae.

Refer *non-symbiotic nitrogen fixation and nitrogen fixation by blue-green algae* part in article 10.2

4. Describe the mechanism of nitrate reduction in plants.

Refer article 10.4

5. What do you mean by transamination? Give a detail account of the mechanism of transamination in plants.

Refer article 10.5 (ii)

6. Give a critical account on the theories proposed for the synthesis of protein.

Refer article 10.6

7. Describe briefly the mode of synthesis of acids in a green leaf.

Refer article 10.5

8. Describe the problem of specificity of amino acid sequence in the protein molecule. Discuss the role of nucleic acid in this process.

Refer topic *role of nucleic acid in protein synthesis* in article 10.6

9. Compare and contrast the "polypeptide hypothesis" with the "template hypothesis."

Refer article 10.6 (a) and (b)

10. In a particular plant protein the amino acids are found to occur in a definite sequence. How this sequence is maintained when these protein molecules are synthesized.

Refer "*role of nucleic acid in protein synthesis*" in article 10.6

11. Describe the nitrogen cycle in nature.

Refer article 10.7

12. Describe the mechanism of fixation of nitrogen by free living and symbiotic bacteria. Explain the significance of this process.

Refer article 10.2A.

13. Describe the control mechanism of ribonucleic acid in protein synthesis.

Refer *role of nucleic acid in protein synthesis* in article 10.6

14. How many amino acids constitute all life? Name all the sulphur containing as also cyclic amino acids. Give a very brief and general account of their ultimate conversion into proteins.

For first part refer article 1.15C in Chapter 1. For last part refer article 10.6

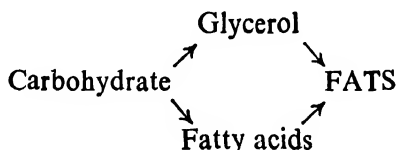
15. Trace the path of nitrogen upto the formation of amino acids.

Refer articles 10.3, 10.4 and 10.5

Fats and their synthesis

11.1 Mechanism of fat synthesis : Fats and fat like substances are present in all living cells of plants and animals as they constitute an important part of protoplasmic system. These fats and other fatty substances are produced in all actively metabolising cells and form a kind of reserve food substance.

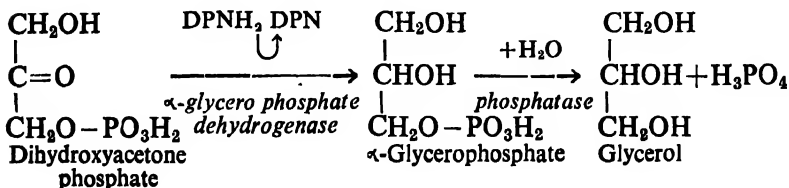
The synthesis of fats generally takes place in the microsomes or endoplasmic reticulum of the cells. Fat synthesis is closely related with the series of chemical reactions that take place during respiration. In the living organism fats are formed by the combination of one molecule of glycerol (trihydric alcohol) with three molecules of fatty acids. Both fatty acids and glycerol molecules are derived from carbohydrate as a result of breakdown during respiration. The general scheme of fat synthesis may be represented as



Hydrolysis of fats catalysed by the enzyme *lipase* shows the formation of fatty acids and glycerol. These products are again converted into carbohydrate or amino acids or used as a source of energy. Both the breakdown and the synthesis of the carbohydrate takes place through the Krebs cycle.

Regarding the synthesis of fats there are three important steps such as (i) synthesis of glycerol, (ii) fatty acids synthesis and (iii) the condensation of glycerol and fatty acids to form ultimately into fats.

(i) *Glycerol synthesis*—Regarding the synthesis of glycerol there are various mechanisms, of which the idea that the dihydroxyacetone phosphate (derived from fructose 1-6 diphosphate during respiration (refer article 15.6 (i) gives rise to α -glycerophosphate and DPN by the influence of the enzyme α -glycerophosphate dehydrogenase and the co-enzyme DPNH_2 runs as follows.



Then dephosphorylation of α -glycerophosphate takes place, in which α -glycerophosphate is converted to glycerol and phosphoric acid by the influence of water and the enzyme *phosphatase*.

This is sometimes referred to as Neuberg's "second form" of fermentation, the first being the production of alcohol and carbon dioxide.

(ii) *Fatty acid synthesis*—In healthy plant tissues fatty acid molecules are present in traces only. There is no definite mechanism regarding the synthesis of fatty acids from carbohydrates in plant cells. It is generally considered that fatty acids are synthesized step by step from 2-carbon unit (acetyl-coA).

The role of acetyl-coA in the synthesis of fatty acids has been made by Barker, Stadtman, *et al* (1949-51) in *Clostridium kluyverii*. These investigators showed that the 2-carbon units condensed to form 4-carbon compound which further condensed with another 2-carbon unit to form a 6-carbon compound and so on until the even-number chain length of 16-carbon compound is reached.

Recent workers on this line suggest that two enzyme-complexes and five co-factors (ATP, NADPH, Mn^{++} , CO_2 and biotin) are essential for the synthesis of fatty acids. According to Lynen (1959) it is now clear that malonyl-coA is formed from acetyl-coA and carbon dioxide through the agency of enzyme system, ATP and the vitamin (biotin). This malonyl-coA now reacts with acetyl-coA to form aceto acetyl-coA which is subsequently being reduced to β -hydroxyacetyl-coA and further to butyryl-coA and ultimately in the formation of butyric acid. The reaction sequence shown in Fig. 11.1 summarizes the recent knowledge of fatty acid synthesis in higher plants.

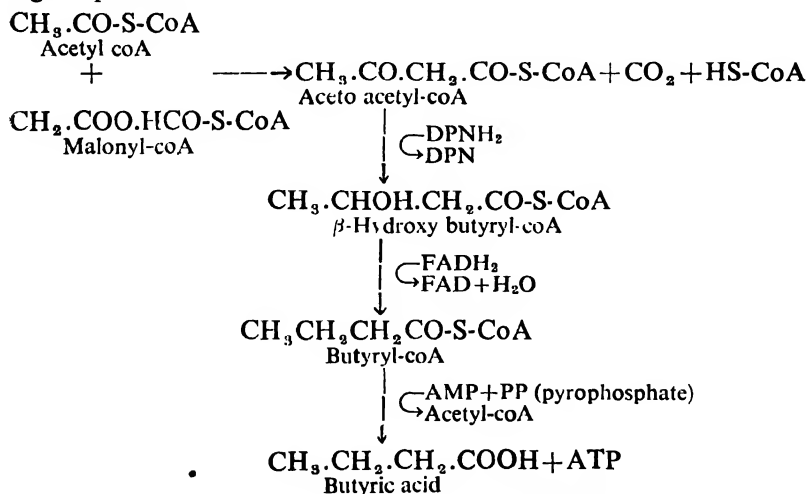


Fig. 11.1 Showing the reaction sequence in the fatty acid synthesis in higher plants.

The schematic representation of the whole system of fatty acid synthesis is given in the following diagram (Fig. 11.2) which shows that the acetyl-coA is both the precursor of the fatty acid synthesis and the product of the fatty acid breakdown.

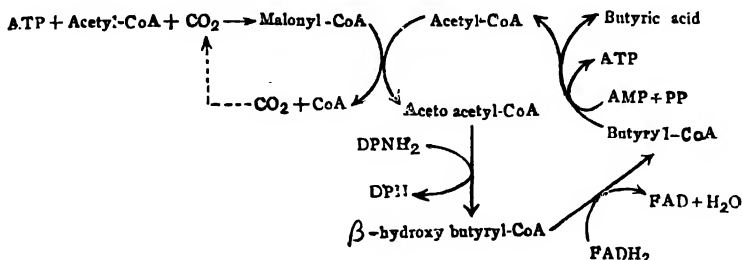
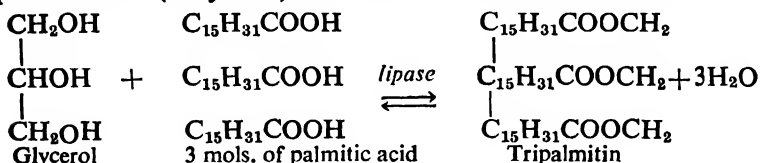


Fig. 11.2 Schematic representation of fatty acid synthesis.

(iii) *Condensation of fatty acid and glycerol*—The final stage in the synthesis of fat involves the condensation of fatty acids with each of the three alcoholic group of glycerol. This type of condensation is termed *esterification*.¹ The most common example of such a synthesis is the formation of tripalmitin (fat) from glycerol and palmitic acid (fatty acid) and the reaction can be shown as :



It is evident from the above reaction that one molecule of glycerol combined with three molecules of fatty acids (palmitic acid) by the influence of enzyme *lipase* to give rise to one molecule of fat (tripalmitin) together with the liberation of three molecules of water.

11.2 Tests for fats : Refer topic *tests for fats* in Chapter 1 article 1.15B.

SELECTED QUESTIONS

1. Elucidate briefly the process of fat metabolism in plants.

Refer article 11.1

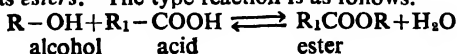
2. Describe briefly the modern theories for the triglyceride structure of natural fats.

Refer article 11.1

3. Describe the process of fatty acid synthesis.

Refer article 11.1(ii)

¹ It is a type of reaction between an alcohol and an acid and the product is usually known as *esters*. The type reaction is as follows.



The role of carbon, hydrogen and oxygen in the synthesis of carbohydrate, fats and related compounds are important in the life of the plant. In addition to these three elements plants require a wide variety of elements which are usually grouped together under the class **mineral elements**. The source of these elements is mainly the ions present in the soil solution and absorbed by the root system. Out of over 105 elements so far discovered, only about twenty or so have been found to be essential for plant growth and metabolism. Apart from carbon, hydrogen, oxygen, nitrogen, sulphur and phosphorus which are constituents of proteins and thereby of protoplasm, there are fourteen other elements which are essential for the growth of some plant or plants viz. calcium, magnesium, potassium, iron, sodium, cobalt, vanadium and silicon. All of these are not required by all plants, but all have been found essential to some.

An *essential element*¹ is one without which the plant cannot complete its life cycle. A guide to the basic chemical requirements for the normal growth of the plants can be obtained in the result of the water culture experiments. To find out which of the elements are essential, the plants are grown in jars containing sterile solution of known chemical composition. One of the first mineral nutrient solutions prepared for the normal growth of higher plants by Knop in 1830, contained only three salts—calcium nitrate, potassium phosphate and magnesium sulphate. These six elements with calcium, potassium and magnesium as cations and nitrate, phosphate and sulphate as anions combined with each other in various ways together with carbon, hydrogen and oxygen are required in large quantities by the plants.

Since about 1920 considerable attention has been focussed and with the discovery of more pure mineral elements it has been shown that the Knop's three salt solution is not complete for the normal growth of the plants. It has been shown that beside the above elements, plant requires a number of other elements like boron (B), zinc (Zn), manganese (Mn), copper (Cu) and molybdenum (Mo),

¹ According to Arnon, an element is considered essential when,

(i) a deficiency of the element make it impossible for the plant to complete its life cycle (vegetative and reproductive) ;

(ii) only by supplying the element in question the characteristic deficiency symptoms can be prevented or corrected ; and

(iii) the element is directly involved in the nutrition of the plant, quite apart from its effects on the microbiological or chemical condition in the soil or culture medium.

which are indispensable for the normal development of plants. Due to their extremely small concentration of these elements required in nutrition they are variously termed as minor or micro or trace elements.

A trace or micronutrient element is required in minute quantity and its role is catalytic, primarily as part of enzyme systems. In the enzyme system, the micronutrient elements act either as activators or as an integral part of the enzyme. For example, manganese is an activator, while zinc, copper, iron and molybdenum are components for enzymes.

TABLE 7

The enzymes either contain the metal or are activated by it.

<i>Metal</i>	<i>Enzyme</i>	<i>Metal</i>	<i>Enzyme</i>
Ca	Lecithinases A and C Lipases Plasma transglutaminase	Mg	Peptidases Phosphatases ATP-enzymes
Co	Peptidases Arginase	Mn	Arginase Dipeptidases Phosphoglucomutase
Cu	Tyrosinase Phenol oxidase Ascorbic acid oxidase	Mo	Nitrate reductase Xanthine oxidase
Fe	Cytochrome enzymes Catalase Peroxidase Tryptophan oxidase	Zn	Lactic dehydrogenase Carboxypeptidase Carbonic anhydrase

On the basis of such water culture experiments it was concluded that besides carbon, hydrogen and oxygen (when supplied in the form of carbon dioxide and water), six other elements—calcium, potassium, magnesium, nitrogen (as nitrate), phosphorus (as phosphate) and sulphur (as sulphate) are essential for normal plant growth. Besides these nine elements, plants also require several other elements like boron, cobalt, manganese, zinc, molybdenum and copper in very minute quantities. The former nine essential elements are termed as bulk or macro elements. Whereas the latter elements are required in traces and are termed as trace or micro elements.

Absence of any one of these elements from the nutrient will cause the plant an unhealthy appearance and will produce typical "deficiency symptoms."

12.1 Absorption of mineral substances : Refer Chapter 4, article 4.9.

12.2 General role of mineral elements : Mineral elements as such cannot participate in any physiological process of the plant, but are only effective when present in an ionic form. On the whole

mineral elements perform a number of functions, the most important of which are as follows :

(i) *Constituents of protoplasm and cell walls*—Some of the mineral elements enter into the composition of the cell. Carbon, hydrogen and oxygen form important component of cellulose, lignins and various reserve foods and major part of the protoplasm in plants. Besides these the role of sulphur in protein, magnesium in chlorophyll, phosphorus in nucleoprotein, calcium in calcium pectate have been well established.

(ii) *Catalytic effect*—Some elements act as catalyst in many metabolic processes of the plants. Some of them act as enzyme precursors, while some others like manganese, magnesium, cobalt etc. act as activators or inhibitors in the enzymatic system.

(iii) *Balancing effect*—Certain elements counteract the toxic effect of some other elements by maintaining an ionic balance. This behaviour of one ion in reversing the usual effect of another ion is also called *antagonism*. Ca, Mg and K belong to this group of elements and are termed as '*balancing elements*'.

(iv) *Influence on acidity and buffer action*—The mineral elements have a great influence on the pH of the cell sap. Some of the important buffer systems in plants, phosphate and carbonate have been found to be originated from some of the elements absorbed by the plants from the soil.

(v) *Influence on permeability of cytoplasmic membranes*—Some elements have a great influence on the permeability of the cell membranes. Thus calcium and other di-or trivalent cations usually have an inhibiting effect on the permeability of the cytoplasmic membrane, where as the monovalent ions have an enhancing effect.

12.3 Specific role of macro elements in plants :

(1) **SULPHUR (S)** : It is mainly absorbed by roots as sulphate (SO_4^{--}) ions, but in some cases very small amount may enter through leaves as sulphur dioxide (SO_2), if it is present in atmosphere. In whatever form it may enter it is in a highly oxidised form which is subsequently reduced to the form of sulphydryl ($-\text{SH}$) group and disulphide ($-\text{S}-\text{S}$) linkage.

Sulphur is a constituent of large number of amino acids in plants (like cystine, cysteine and methionine) which are ultimately built up into proteins. It is also an important constituent in the formation of mustard oil glycosides (*sinigrin*) which give the characteristic odour and flavour of mustard, onions, garlic etc. It is also a constituent of two important plant hormones—thiamine and biotin.

The role of sulphur in the effective N_2 -fixation by the root nodule organisms have been shown by Anderson and Spencer (1949). Sulphur metabolism is therefore linked with the N_2 -fixation and possibly with the reversal of this process.

It forms an important constituents of certain vitamins, co-enzyme A and glutathions.

It increases the oil content of some crop plants such as flax, soyabean, peanuts etc.

Symptoms of deficiency : Like nitrogen deficient plants, there is a general *chlorosis*, followed by the production of anthocyanin pigments in the sulphur deficient plants. Sulphur starvation results in shortage of proteins in plants. Other effects of sulphur deficient plants are the extensive development of root system, a hard woody stem and accumulation of nitrates and carbohydrates.

(2) PHOSPHORUS (P) : It is mainly absorbed by roots as primary ortho-phosphate (H_2PO_4^-) ions. Smaller amounts of phosphorus are also absorbed as the secondary ortho-phosphate (HPO_4^{--}). Unlike nitrogen and sulphur, phosphorus, however, is not reoxidised in plant tissues but is linked into organic combination of highly oxidised form. It enters in the composition of nucleic acid (DNA and RNA) and forms part of certain fatty substances, phospholipids.

It is also linked with the energy transfer system within the cell. Such an energy riched compound is adenosine triphosphate (ATP), which contains three phosphates together with other complicated ring structure. Removal of two terminal phosphate bonds yields much more energy than does removal of first phosphate group. Phosphorus is also present in large amounts for the synthesis of nucleoproteins.

The role of phosphorus in plant metabolism is closely connected with that of nitrogen metabolism. Lower the concentration of phosphorus in soil greater is the absorption of nitrates.

Phosphorus compound recently been identified in pyridoxyl phosphate, an enzyme for transamination in plants and animals.

Symptoms of deficiency : Decrease in the rate of protein synthesis is the general symptom of phosphorus deficient plants. It also causes the accumulation of carbohydrates and soluble nitrogenous compounds. Like nitrogen, other important symptoms of phosphorus deficient plants are the premature leaf fall and accumulation of purple anthocyanin pigment.

(3) CALCIUM (Ca) : It is absorbed as the Ca^{++} ions. The main role of calcium is in the rigid and stiff appearance of the cell wall and helps the formation of middle lamella. There are two ways by which Ca may give proper rigidity to the cell. The older idea suggests that Ca may unite with pectic acid to form calcium pectate—which is an essential part for the middle lamella of the cell wall. According to the recent concept the rigidity of cell wall is due to the proper balance of K-ions and Ca-ions which give a correlation between Ca-ions and turgor and consequently rigidity of the cell walls.

Calcium also plays an important role in the reduction of nitrates in plant tissues during nitrogen metabolism.

With organic acids calcium forms salts that combine with protein molecule. According to Sorokin and Summer (1940) suppression of mitotic cell division takes place in the absence of Ca. Synthesis of some of the organic acids also takes place as a result of absorption of Ca. Antagonistic effect of many single salt like Na, K, Mg is reduced by the presence of Ca.

Symptoms of deficiency : Growth in the meristematic regions of stem, leaf and root is greatly affected by the deficiency of calcium. Thus the extreme effect of such deficiency is the death of the apical regions and the consequence is the decrease in the growth of these organs. Margins of the younger leaves generally show the peculiar chlorotic behaviour.

(4) **MAGNESIUM (Mg)** : It is absorbed in the form of the Mg^{++} ion. Magnesium is one of the essential mineral constituents of chlorophyll molecule where Mg combines with iron containing precursor to a molecule of chlorophyll. It also plays an important role in the phosphorus metabolism of plants and also linked up with the synthesis of nucleoprotein and respiratory mechanism.

Mg acts as specific co-factor for several enzymes (e.g. *trans-phosphorylases, dehydrogenases, carboxylases* etc.) present in plant cells. Dixon states that all *phosphokinases* depending on -SH group are activated by Mg. This enzyme causes phosphorylation of glutamic acid by ATP prior to the formation of glutamine.

Symptoms of deficiency : *Chlorosis* of the leaves is the general symptom of magnesium deficient plants. The older leaves are affected earlier than the younger leaves. Thus development of anthocyanin pigments with necrotic spots is the ultimate effect of magnesium deficiency.

(5) **POTASSIUM (K)** : It is absorbed as the K^+ ion. Although potassium does not enter into the chemical composition of any organic compound in the plant, its role in plant metabolism is no less important. It is mainly present in the meristematic tissues and quite absent in the nucleus and plastids.

The main role of K^+ is to decrease the turgor pressure (=the resistance of the cell wall to further expansion), the tissues are therefore flaccid. With increasing flaccidity of the tissues, the stomata close. A poor supply of potash leads to an inhibition of photosynthesis.

By changing the hydration of the cells potash deficiency leads to increased activity of the hydrolyzing enzymes (=catabolic enzymes) present in the cytoplasm and consequently to an accentuation of the catabolic processes.

The enzymes functioning in respiration require K^+ as a sort of *essential co-factor* in order to be able to develop their activities to the full extent. These are mainly processes such as oxidative phosphorylation (phosphate transfer) or the activation of a substance by means of adenosine triphosphate (ATP) etc.

Potassium deficiency is also equivalent to nitrogen-excess. i.e., plants suffering from K^+ deficiency are forced to absorb nitrogen in more than optimum quantities. Its deficiency also leads to an accumulation of ammonia and amino acids, because the energy for the construction of amides or protein is lacking.

Symptoms of deficiency : Inhibition of protein synthesis is the main symptoms of potassium deficiency and which results in the accumulation of organic nitrogenous compounds in the plant cells. Carbohydrate metabolism is inhibited due to lack of potassium. Increase in the respiratory rate is also another effect of potassium deficient plants.

Among the external symptoms, the scorched leaf tips and dull yellow margins of the leaves are important. Accumulation of large amounts of carbohydrates is decreased in the underground stems of potatoes and sugarbeets, this is probably due to checking of enzymatic reaction to hydrolyse starch into soluble sugars in the leaves.

(6) NITROGEN (N) : The most important role of nitrogen in the growth and metabolism has been well investigated. Nitrogen is an important constituent of a number of organic compounds in plants. It is present in many of the vitamins, purines and in the alkaloids. It forms a major and indispensable constituent of protein and nucleic acid which play the important role in the metabolism, growth, transmission of heritable character etc. Since life is characterised by the association of proteins, the role of nitrogen in relation to its constituents of protein and nucleic acid is vital.

Besides this essentiality, nitrogen forms an indispensable ingredient of the food of animals and which they obtain from plants. Plants actually convert the soil nitrogen into forms suitable for animal nutrition. A detail account of this has been given in Chapter 10.

Symptoms of deficiency : The yellowing of leaves (*chlorosis*) is the main symptom of nitrogen deficient plants. The growth of the plant is generally stunted. Late formation of flowers is also another symptom. Formation of purple pigment, anthocyanin in the leaf petioles, veins and stems of the plants is also another symptoms of nitrogen deficient plants.

12.4 Specific role of micro elements in plant metabolism : Considerable attention has been paid in recent years regarding the functions of the micro elements : especially their role in the catalytic reactions. Since they are required in only small quantities, their catalytic role particularly in the enzyme systems is quite obvious. A large number of evidence indicates that their participation in enzyme systems can be grouped into two categories ; (a) those in which the metal has been shown to be an integral part of the enzyme and (b) those in which the metals act as activators. Nason and McElroy (1963) showed that zinc, copper, iron and molybdenum are the important components for enzymes whereas manganese acts as an activator.

The detail specific physiological and biochemical functions of the micro elements are given below.

(1) BORON (B)¹ :

Symptoms of deficiency :—A variety of symptoms can be exhibited by the deficiency of boron which may be described as 'top-sickness' of tobacco ; 'hollow heart' of peanut ; 'yellows' of alfalfa ; 'heart rot' of beet etc. (Hewitt, 1963). Boron deficiency also causes the young leaves of wheat to become white and sometimes to roll. In some cases the leaf tip of wheat appears corrugated and may split. In some plants red and purple tints develop.

A large number of sterility and malformations of reproductive tissues may be observed in boron deficient plants.

Physiological role :—Boron is absorbed in one or more of its ionic forms viz $B_4O_7^{--}$, $H_2BO_3^-$, $H_2BO_3^{--}$ or BO_3^{--} . The exact role of boron in plant metabolism is still incompletely known. The growth and development of some plants are influenced by this element in a very minute concentration, higher concentration results in the toxicity of plant tissues. Since boron forms a complex with sugar and related molecules it has been suggested that its role may be involved in sugar transport (Gaugh and Dugger, 1954) although it may not be direct (Albert, 1965).

Boron is not a specific activator of any enzyme system (Nason McElroy, 1963).

According to Jordan and Anderson boron stimulates nitrogen fixation by *Azotobacter* to some extent.

The effect of boron on calcium uptake has been observed by Henderson. It also plays a role in the development of roots and also in the root nodules in leguminous plants.

Recent work in Russia has shown that shortage of boron decreased RNA and DNA content in stem and root tip of sunflower, indicating the possible role of boron in nucleic acid metabolism.

(2) MANGANESE (Mn) :

Symptoms of deficiency :—A large variety of chlorotic patterns and necrotic spotting have observed during manganese deficiency. Deficiency of manganese causes brown lesions in barley, 'grey speck' in oats and white necrotic streaks in wheat and rye (Hewitt, 1963). Its deficiency also causes a characteristic sunken-brown necrosis at the centre of the cotyledons of pea.

Photosynthesis is reduced in Mn-deficient plants and a reduction of oxygen evolution has been shown to be a result of deficiency.

Physiological role :—Manganese is absorbed by the plant as

¹ Boron differs from other micro nutrients in that it never involves any enzyme system and is absorbed in anion form rather than cation like other mineral nutrients.

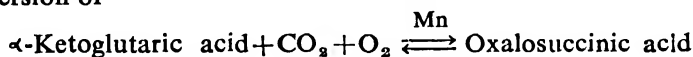
manganous ion (Mn^{++}) and also in molecular combinations with certain organic complexing agents e.g. EDTA.¹

Manganese plays an important role in the nitrate assimilation by green plants (Nason and McElroy, 1963). The basis of this implication is that Mn serves as an activator for hydroxylamine and *nitrate reductases*.

Manganese helps in the dehydrogenation. Thus the whole isocitric dehydrogenase and pyruvic dehydrogenase system are activated by Mn. Many decarboxylations are of oxidative and non-oxidative type and also involve Mn. In presence of Mn the following reversible oxidative decarboxylation takes place.



The example of non-oxidative decarboxylation is exhibited in the conversion of



Manganese functions directly or indirectly in chloroplast formation.

(3) ZINC (Zn) :

Symptoms of deficiency :—Leaves of Zn-deficient plants are yellow to dull olive-green in colour showing the characteristic chlorosis. Sometimes Zn-deficiency resembles very much the phosphorus deficiency symptoms.

Changes in the leaf morphology and cell histology are the characteristic features of Zn deficiency. Some of the important morphological disorders are little leaf and 'rosette' of apple, peach etc. ; 'mottle leaf' of citrus, white bud of corn etc. Reduction in the internode length of apple, cotton, flax, tomato, bean, rubber etc. is also due to lack of zinc in the plant body.

Some irregular necrotic areas develop in vascular tissues in the leaves of tomato, tobacco, corn and cotton due to Zn deficiency.

Hewitt (1963) showed that the seed production is severely decreased due to Zn deficiency. In citrus fruit size is also reduced very much.

Zn deficiency causes delay in the differentiation of tissues, decreases palisade cells and increases the size of the cells (Hewitt, 1963). Deficiency also causes the decrease in the number and size of the plastids. In tomato all cells including those in the meristematic zone are enlarged prematurely. Mitochondrial particles are very much distorted. Plastids in many cases are more vacuolated and disintegrated in Zn-deficient plants.

Reed (1946) showed that Zn deficiency resulted in the accumulation of inorganic phosphate (PO_4). A number of amino acids are found to be increased by Zn deficiency (Possingham, 1956).

¹ EDTA—Ethylene diamine tetraacetic acid.

Physiological role :—Zinc is absorbed as Zn^{++} ion and also as a complex with EDTA. This element is required in a very minute quantity for normal growth and development ; higher concentration results in toxicity.

Zinc is found to activate the enzymes *dehydrogenase* and *tripeptidases*. Zn also causes the synthesis of *diphosphopyridine nucleotidase* (DPNase), an enzyme which splits DPN at the nicotinamide riboside linkage.

Zinc is also important for the synthesis of tryptophane which is the precursor of growth hormone indole acetic acid (IAA).

Nason and McElroy (1963) have shown the impaired fruit setting and seed production due to Zn deficiency.

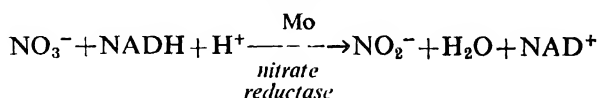
In fungi, zinc helps not only to increase the uptake of calcium, phosphorus and magnesium but also the efficiency of sugar utilization.

(4) MOLYBDENUM (Mo) :

Symptoms of deficiency :—A bright green or pale orange colour of the leaves due to interveinal mottling is the symptom of Mo deficiency. In severe case it causes necrosis. Flower formation and seed production is very much decreased due to Mo deficiency. In some cases seeds may fail to develop.

Leguminous plants require a considerable amount of molybdenum, shortage of which causes leaf falling, wilting and marginal rolling and desiccation.

Physiological role :—It is possibly absorbed as MoO_4^{--} ions. The possible role of molybdenum in an electron transfer system for the reduction of nitrate to nitrite in the presence of *nitrate reductase* in *Azotobacter* and *Nostoc* has been well substantiated.



Molybdenum is an integral part of this enzyme. Mo is also involved in the phosphatase enzymes. It also helps in the formation of enzyme-substrate complex although the actual details of reactions involving chelate formation are not yet known.

(5) COPPER (Cu) :

Symptoms of deficiency :—The most important deficiency symptom of copper is the summer 'dieback' when the leaves become twisted and curved. In many cases the plants show interveinal chlorotic mottling. In citrus the leaves and bark stain brown and followed by 'dieback' of the shoot with the production of characteristic multiple buds.

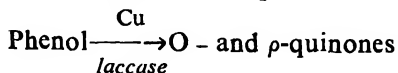
In tomato, necrosis and withering takes place in old leaves.

In cereals, excessive weak tillering is the characteristic symptom of copper deficiency.

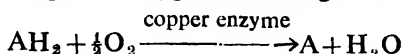
According of Possingham (1956) Cu deficiency causes a marked change in the amino acid content within the plant. High nitrogen and protein status was found in Cu-deficient plant.

Physiological role :—Mainly absorbed as the cupric ion (Cu^{++}). It forms an important component of a number of oxidising-reducing enzymes like *polyphenol oxidase*, *laccase* and *ascorbic acid oxidase* (Nason and McElroy, 1963).

Thus the activity of the enzyme *laccase* is found to be increased by Cu in the conversion of phenol to quinones.



Copper enzyme acts as a catalyst in the direct oxidation of the substrates by atmospheric oxygen according to the following equation.



Thus the copper enzymes are believed to have a significant role in terminal respiration in some plants.

Hill suggested that Cu might be needed for the formation of iron-porphyrin, a precursor of chlorophyll.

Cu also plays an important role in the biogenesis of anthocyanins by *Spirodella* (Edmondson and Thimann).

(6) IRON (Fe) :

Symptoms of deficiency :—The most important deficiency symptom of iron is chlorosis caused by a decrease in chlorophyll content, although the pattern of symptom varies with species.

Jacobson (1957), Hewitt (1963) and Nason and McElroy (1963) showed that the size of the chloroplasts decreases considerably due to iron deficiency.

Iron deficiency also caused a cessation of cell division in the apical meristem of pea roots causing a considerable increase in the protein content of the iron-deficient roots.

Increased citrate is of general occurrence in the iron-deficient plants, but the exact relationship is not known.

Physiological role :—Its main role is the formation of iron-porphyrin, a precursor of chlorophyll has been well established. Although chlorophyll does not contain iron, synthesis of chlorophylls is dependent upon its presence.

Iron is believed to have a significant role in the terminal respiration of some plants which involve the transfer of electrons to molecular oxygen. It is mediated exclusively by the iron-porphyrin, containing series of cytochromes like *a*, *a*₃, *b*, *b*₅, *c* and *c*₁. During electron transport iron of cytochrome continuously undergoes oxidation and reduction between ferric and ferrous forms (Nason and McElroy, 1963).

TABLE 8

Information about elements essential for higher plants

<i>Element</i>	<i>Important roles</i>	<i>Deficiency symptoms</i>
Nitrogen (N)	Component of amino acids, proteins, nucleic acids, ATP, Coenzymes, Chlorophylls etc.	Stunted growth, chlorosis, leaf fall, anthocyanin formation; older leaves most affected.
Phosphorus (P)	Component of nucleic acids, nucleotides, phospholipids, sugar phosphates, ATP, coenzymes etc.	Stunted growth, dark blue-green leaves, anthocyanin, maturity delayed, older leaves most affected.
Potassium (K)	Enzyme activator, required for protein synthesis, stomatal function.	Necrosis, mottled chlorosis, weak stems; older leaves most affected.
Calcium (Ca)	Middle lamella component, membrane structure and permeability, α -amylase component.	Necrosis of root and shoot tips, stunted growth, younger leaves most affected.
Magnesium (Mg)	Chlorophyll component, enzyme activator, maintains ribosome structure	Mottled leaf chlorosis, leaf tips turned up; older leaves most affected.
Iron (Fe)	Component of cytochrome and ferredoxin, enzyme activator, chlorophyll synthesis.	Chlorosis of young leaves between veins, short and slender stems.
Sulphur (S)	Component of protein, thiamine, biotin and coenzyme A.	Chlorosis of young leaves between veins.
Boron (B)	Carbohydrate translocation, prevents phenolic acid accumulation and toxicity.	Black necrosis of stem and root tips, swollen roots, leaves twisted.
Manganese (Mn)	Enzyme activator, catalyst, electron carrier.	Chlorosis except along smallest veins, necrosis between veins, younger leaves most affected.
Zinc (Zn)	Synthesis of IAA and chlorophyll, component of some enzymes.	Chlorosis, stunted leaves and internodes, distorted leaf margins, older leaves most affected.
Copper (Cu)	Nitrate reduction, electron carrier, component of some enzymes.	Young leaves distorted, dark green, wilted.
Molybdenum (Mo)	Nitrogen fixation, electron carrier.	Chlorosis, necrosis and distortion of young leaves.

The energy required for salt uptake and accumulation is mediated by the heme-containing system.

Its role in nitrogen fixation is due to iron-porphyrin-protein complex.

An enzyme thought to contain iron-prophyrin structure is responsible for auxin destruction (Tang and Bonner, 1947).

(7) COBALT (Co) :

Little evidence is available regarding the necessity of cobalt for non-leguminous higher plants although it may greatly influence the metabolism and growth of the tomato and rubber plants.

The most useful effect of cobalt in blue-green algae as well as in higher plants seems to be related to nitrogen fixation. Cobalt activates some plant enzymes like *peptidases* and vitamin B₁₂.

It produces a stable cystine-cysteine Co⁺⁺ complex with the formation of free cysteine.

Nickerson (1948) showed that yeasts accumulated Co in an organic complex.

(8) VANADIUM (V) :

No direct evidence is available regarding the necessity of vanadium for higher plants. Though the application of vanadium in the soil increases the yield of legumes, still it does not prove its necessity for plant growth (Harris, 1962). Arnon (1953, '58) showed that vanadium is essential for *Scenedesmus obliquus* and its deficiency lowers the chlorophyll content and affects the rate of photosynthesis in this alga.

SELECTED QUESTIONS

1. Give the classification of mineral elements indicating their essentiality.

Refer *introduction* of Chapter 12

2. Write a short essay on the mineral nutrition of plants.

Refer *introduction* of Chapter 12 and articles 12.1 and 12.2

3. Discuss the role of the following elements in the metabolism of plant :—

- (i) phosphorus (P)
- (ii) potassium (K)
- (iii) sulphur (S)
- (iv) iron (Fe) and
- (v) magnesium (Mg)

Refer articles 12.3 and 12.4

4. What are trace elements? Mention the names and function of each of them.

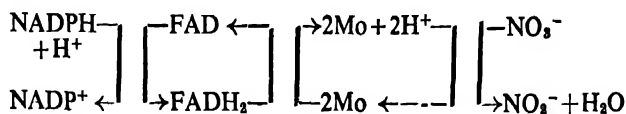
Refer article 12.4

5. Give the physiological role of boron (B) and molybdenum (Mo). How do they help in nitrogen fixation and reduction in leguminous plants.

Refer article 12.4 (i) and (iv) and for the last part of the question add :

The role of boron and molybdenum in nitrogen fixation have been investigated by a number of workers and they showed that *Azotobacter* and other nitrogen fixing organisms require trace amount of boron and molybdenum salts for nitrogen fixation and growth. 1 ppm of one of these metals is sufficient for an optimal effect. Another role of these metals is in the reduction of nitrate to nitrite catalysed

by the enzyme *nitrate reductase*. The enzyme appears to be a molybdoflavoprotein (Nicholas *et al*, 1955) which appears to catalyse electron transfer in the following sequence,



and leads to the reduction of nitrate to nitrite. Thus this provide an explanation for the long known requirement of this element in the metabolism of various plant and microbial cells.

6. What are trace and tracer elements ? Describe the role of them in plant physiology.

For trace element refer introduction part of Chapter 12 and for their role refer article 12.4. For tracer element refer topic *detection of radioactivity* in Chapter 1 article 1.5

7. What are micronutrients ? Give a brief account of the role of micronutrient elements in the nutrition of plants.

Refer article 12.4

8. Write notes in the role of molybdenum in plant nutrition.

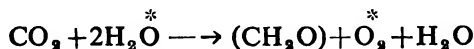
Refer role of molybdenum in article 12.4 and also question 5

Special Method of Nutrition

Biochemical studies reveal that various types of molecules are necessary for structure, maintenance and function of the plant cells. There is considerable variation among the organisms in their capacity to manufacture these complex organic substances within the body. Some plants are unable to synthesize many of the essential growth factors for such organism. The study of this growth requirement is called **nutrition**. Organisms are divided into two major groups, *autotrophic* and *heterotrophic*, on the basis of their mode of nutrition. The former includes all the green plants that are able to obtain their food from the inorganic materials, while the latter i.e., heterotrophs get their ready-made food from the bodies of other organisms.

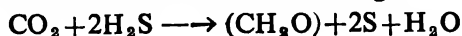
13.1 Autotrophic organisms : Autotrophic plants are able to absorb carbon dioxide of the atmosphere, water and inorganic salts from the soil and can synthesize complex substances for the building up of their body. On the basis of their energy requirement they are grouped into (i) photosynthetic autotrophs and (ii) chemosynthetic autotrophs.

Photosynthetic autotrophs—The light energy is converted into chemical energy by photosynthesis which is actually utilized by this group of plants for their synthetic activities. The main groups of photosynthetic autotrophs are the complex green plants, different groups of algae and coloured sulphur bacteria. The various colour combination of these plants is due to presence of a mixture of different pigments in varying proportion. The important pigment which is present in all these cases is chlorophyll—the green pigments of the plants. Chlorophylls are able to capture light energy and convert it into chemical energy for synthetic activities. The light energy is combined with carbon dioxide and hydrogen—derived from water, H_2S and other sources and builds the energy rich compound (carbohydrate) which is said to be the sole source of energy for all living organisms. The general scheme for photosynthesis in green plants is as follows



Water is the main hydrogen donor for photosynthesis and which reduces carbon dioxide upto the level of carbohydrate (refer Chapter 9 article 9.4).

In case of sulphur bacteria, H_2S is the hydrogen donor and which ultimately reduces carbon dioxide according to



Another difference between these two types of reaction is that oxygen is not produced as one of the end products in the second reaction, instead elementary sulphur is produced.

Chemosynthetic autotrophs—They obtain their energy from the oxidation of some inorganic substances and utilize it in the synthesis of all their protoplasmic constituents. The most important chemosynthetic autotrophs are *Nitrosomonas* and *Nitrobacter*.

Both of these bacteria are present in the soil and *Nitrosomonas* can covert ammonia to nitrite within the soil (refer article 10.2).



The *Nitrobacter* converts nitrite to nitrate. The energy that is liberated due to above conversion is utilised by these bacteria for the synthesis of complex carbohydrate or nitrogenous compounds. The other bacteria of this group are iron and sulphur bacteria which also obtain their energy from oxidation of inorganic substances and the energy is utilized for the various synthetic activities.

13.2 Heterotrophic organisms : Heterotrophic plants are those which cannot prepare their food from inorganic raw materials like the autophytes. The heterotrophic plants get organic materials either from the bodies of living organisms or from dead bodies of plants and animals. Heterotrophic mode of nutrition is present in all groups of plants and specially among fungi and bacteria.

Heterotrophic plants include saprophytes, parasites, insectivorous plants etc.

(i) *Saprophytes*—The nutrition of saprophytes is known practically from the bacteria and fungi including moulds and basidiomycetes that grow on non-living organic material. Saprophytic fungi use large amount of carbon as source of organic food. Some saprophytic organisms use paraffin as a source of carbon. The nitrogen is mainly absorbed by saprophytic fungi in inorganic form as ammonium nitrate. There are some variations regarding the utilization of different organic nutrients. Sugar is readily absorbed by most of the moulds as non-nitrogenous compounds. Little is known regarding the fate of the organic compounds that are absorbed by saprophytes. Some of the enzymes that are also present in autotrophic plants possibly play an important part. While saprophytes absorb carbon as carbohydrates and nitrogen as nitrates and ammonium salts, the fate and synthesis of these elements may possibly follow the same path as in autotrophic plants.

Among the flowering plants, orchids and *Monotropa* grow in the forest soil which is rich in humus. These plants grow always in association with mycorrhizal fungus and obtain food materials from the humus with the help of mycorrhizal fungus.

(ii) *Parasites*—They obtain their food mostly from living plants and animals. The plant or animal which supplies them with food is known as *host*. They include mostly fungi and bacteria—a few angiosperms

are also parasites. The entry of fungal parasites generally takes place with the help of enzymes produced by the parasites, such enzymes or toxic substances dissolve the cell wall of the host plant. After penetrating, parasites spread through the vessels, destroy the lignified tissues and thereby obtain their nutrition. In some angiospermic parasites like *Cuscuta*, *Lathraea* etc., the roots produce haustoria which penetrate the host tissues and come in contact with xylem and phloem of the host. From this xylem and phloem water and solutes are absorbed by parasites and then are translocated to body. Besides *Cuscuta*, there are other parasites which grow on the roots of certain plants. These are called *root-parasites* and the common example is *Orobancha*. Besides these there are several green coloured partial parasites known as *hemi-parasites* found in some genera of the family Scrophulariaceae. They live by getting dissolved salts and water for their own food. The photosynthetic activity of leaves of *hemi-parasites*, except in few cases seems to be normal. The leaves of some *hemi-parasites* e.g. *Viscum album* are green and photosynthesis takes place normally ; hence Pierce suggested that there is only a contact between the xylem of the host and haustoria of the parasites.

(iii) *Symbiosis or mutualism*—In the plant kingdom a close association of individuals of different species for their mutual benefit has been noted. Lichens furnish good examples. Some plants of the family Leguminosae also furnish good examples in which small nodules develop on the roots as a result of rootlet infection by some bacteria like *Pseudomonas*, *Bacillus* etc. These bacteria absorb nitrogen from the soil and manufacture some substances which are excreted in the rootlet cells. The bacteria on the other hand get water and salts from the root of such leguminous plants. The association of fungus with the roots of certain plants i.e. *micorrhiza* is also important as the nutritional relationship between the two is maintained, where the associated fungus helps the plant in obtaining water and food materials, especially nitrogenous compounds from the soil and the plant again supply food to the fungus.

(iv) *Insectivorous or carnivorous plants*—The insectivorous plants live in environments deficient of nitrogen and in order to supplement their requirements they are endowed with mechanism to catch and prey upon insects. Beside this special habit, their mode of nutrition in any way differ from the normal autophytic plants. These plants are heterotrophic, sometimes regarded as *hemi-parasites*. They have special apparatus by which they trap small animals and insects. The organic materials from the bodies of such insects or animals are absorbed finally after decay or digestion. In case of *Drosera* (sundew), when insects alight on the leaf, the tentacles present on the leaf bend over the insect and secrete fluid. This secretion contains *protease* enzymes which convert the nitrogenous substances of the insects into amino acids. These amino acids are absorbed finally by the cells of the leaf. In *Utricularia* there is no evidence of

enzyme secretion in the bladders, where trapped animals die and these are finally decomposed by the action of bacteria and then such decomposed products are absorbed by the cells of the wall of bladder or by internal glandular hairs. Regarding the nutrition of pitcher plants (*Nepenthes*), there are several opinions of which the latest idea is that the liquid present in the pitcher contains protease enzymes which help in digestion and the products of digestion are finally absorbed by the glands or by the cells of the pitcher wall. The watery fluid of the pitcher does not come to harbour any bacterial growth, inspite of the presence of insect bodies at different stages of digestion, as it possesses antiseptic properties. Some species of *Nepenthes* produce pitchers on the surface of the ground and such pitchers are efficient for trapping creeping animals like worms, centipedes and leeches.

SELECTED QUESTIONS

1. Distinguish between autotrophic and heterotrophic nutrition and describe the types of heterotrophic nutrition.

Refer *introduction* part of Chapter 13 and for the last part of the question refer article 13.2

2. Describe ways through which saprophytes and insectivorous plants obtain their food.

Refer topics *saprophytes* and *insectivorous plants* in article 13.2

Translocation of Solutes

The green autotrophic plants can manufacture all their requisite amount of organic food-stuff within the body. The green tissues are the main site of their synthesis and the green cells are mainly confined to the leaves. All cells require organic food-stuff for normal growth and development. The non-green parts of the plants therefore must obtain the organic food-stuff from the leaves. Before the food-stuff actually reach the non-green parts, it must pass through the intervening regions. *The movement of organic food-stuff within the plant from the site of synthesis to the site of utilization is known as translocation or conduction of solutes.*

14.1 Translocation of organic materials : It is evident from the earliest evidence that phloem (sieve tube) is the main pathway for the translocation of organic compounds. It is supported from ringing experiment (removal of tissues external to the xylem) demonstrated by a number of workers. Although it is undoubtedly proved that the channel of translocation is the phloem but the way in which the organic substances move in the phloem is a matter of great dispute and also a puzzling problem.

Among the earlier workers in this line may be mentioned the name of Hanstein (1860). He concluded from his experiment (by removing the extra cambial tissues) that the food materials which are synthesized in the leaves and which are also necessary for the formation of adventitious roots, are translocated downwards through the extra cambial tissue i.e., probably through the sieve tubes.

This has been further supported by other workers who showed that there is an active accumulation of starch above the ring together with the microchemical demonstration of sugars and organic nitrogenous compounds in the sieve tubes. These findings allowed the general acceptance of the idea that translocation of organic compounds occurs through the phloem.

These conclusions of the earlier workers have been heavily criticised by Dixon (1923) while studying the accumulation of starch in the developing potato tuber along the cross sectional area of the sieve tubes. Dixon concluded that the sieve tube contents move at a rate of 50 cm per hour while the simple diffusion of sugar molecules takes place at a rate of 0.2 mm per day. These inevitably led Dixon to consider that the main channel of this movement is not the sieve tube but the xylem where the flow of organic compounds takes place like flow of water through a pipe.

It has been observed in later years that although Dixon's observation was very accurate still his conclusion regarding the path of the organic movement was incorrect. The exact path of conduction of organic substances has been found to be phloem by Mason and Maskell (1928) although in their ringing experiment they showed that a certain amount of leakage of metabolites from phloem to xylem takes place. Further work of Mason and Maskell (1928) suggested that movement of the compounds takes place along concentration gradient and the companion cells play an important role in interconversion of sucrose and hexose.

Present knowledge, however, does not permit us to think that the soluble carbohydrates move acropetally through the xylem and phloem ; although xylary transport hypothesis is not tenable.

14.2 Mechanism of phloem transport: The theories put forward to explain the mechanism of phloem transport fall under three main groups although none of them is entirely satisfactory.

(i) *Activated diffusion hypothesis*—This theory proposed by Mason and Phillis (1936) suggests that the protoplasm within the sieve tube helps in hastening the diffusion of solutes and further the mode of activation requires respiratory energy and no experimental evidence in support of this theory has been forthcoming.,

At present it is evident that the sieve tube element does not possess any metabolic machinery responsible for driving the translocation process, except it helps only in the metabolic transfer which move solutes across the membranes.

(ii) *Streaming of protoplasm theory*—De Vries (1885) and more recently Curtis (1935) proposed that the streaming of the protoplasm within the phloem is responsible for the transport of the solutes from one end to the other. Since the sieve tube elements are continuous from one tube to another the theory accounts for the simultaneous movement of the solutes in both the directions (Fig 14.1).

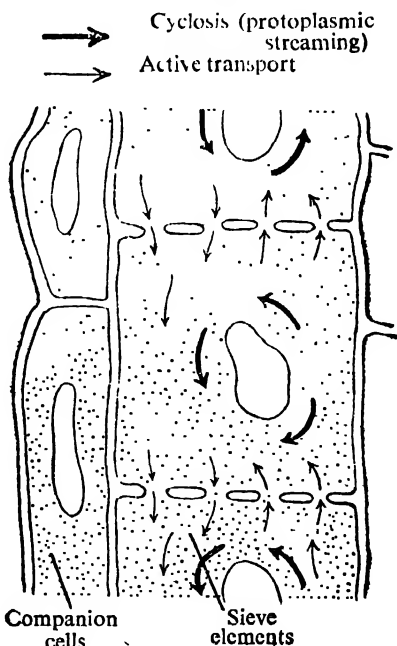


Fig. 14.1 Diagrammatic representation of protoplasmic streaming concept of translocation.

The best evidence for this theory would be the demonstration of simultaneous bidirectional movement within the smallest functional unit of conduction. This has

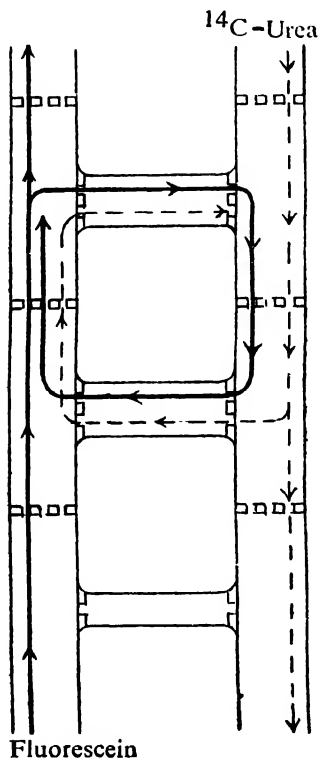


Fig. 14.2 Lateral transport and loop path to explain simultaneous bidirectional movement in a single sieve tube (modified after Eschrich, 1967).

recently been illustrated by Eschrich (1967) by feeding ^{14}C -urea to the upper leaf and fluorescein to the lower leaves of *Vicia faba*. Eschrich's idea regarding the phloem transport has been demonstrated in figure 14.2.

The main drawback of this theory is that although the streaming of cytoplasm is possible in young sieve elements but it is completely lacking in the mature one. Another weakness of this theory is the inadequacy of the definite rates of protoplasmic streaming to correlate it with the known rate of solute transport through the phloem. Further Schumacher's (1936, '37) observation on the movements of fluorescein strongly invalidates this theory. He showed the movements of fluorescein in a opposite direction to that in which the protoplasm itself was moving.

(iii) *The mass flow hypothesis* : This theory was initially postulated in 1860 by Hartwig ; but it was more clearly formulated as a scientific theory by Münch in 1930.

In its original form the theory included all the living cells of the plant, but now-a-days its functioning is thought to be restricted to the sieve tubes.

During photosynthesis carbohydrates are produced and in the translocable form these carbohydrates exist as sucrose. Water which has ascended the stem in the xylem is absorbed by the leaf cells containing high concentration of sucrose as a result of osmotic forces and this in turn brings an increased hydrostatic (turgor) pressure in these cells. At the same time a lowering of the concentration of sucrose in these regions where the assimilates are utilized for growth, storage and respiration results in a lowered hydrostatic pressure. Thus the region of synthesis (green leaves) may be regarded as a 'source' and the region of utilization as a 'sink'. Because of the gradients of hydrostatic pressure so created, there will tend to be a

bulk or 'mass' flow or solution and dissolved solutes from the 'source' to the 'sink' via the phloem.

Such a mechanism may be illustrated by means of a simple physical model (Fig. 14.3).

As shown in the figure the two spherical semi-permeable membranes (A and B) are connected with a tube to form a closed system. Sphere A contains a solution of sugar, while B contains a weaker sugar solution of water and the whole set is placed in water. Osmosis will then cause an inflow of water in both the spheres but a greater hydrostatic pressure will develop in A due to higher sugar concentration and hence water together with sugar solution will flow from

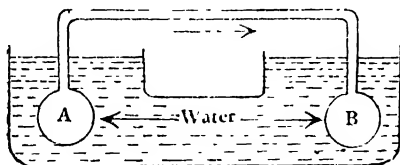


Fig. 14.3 Diagram showing an osmotic system to clarify the mass flow of solution.

A to B through the connecting tube. This will cause a greater diffusion pressure in the water in B than in the pure water in which the spheres are immersed. Water will therefore flow out from B to the surrounding medium and consequently there is a flow of sugar solution from A to B until the concentration of sugar in A and B is equal. To maintain a continuous system sugar must be added to A and should be equally removed from B.

As a result of photosynthesis, a greater osmotic concentration is maintained in the leaf due to synthesis of sugar; this causes a high turgor pressure in the mesophyll cells which allow some of the cell solution into the sieve tubes (Fig. 14.4). A major portion of the solutes moves down the sieve tube and a fraction of it may move laterally to cambium which is again forced into the xylem, join the ascending system of water and again move to the leaf cells, major part of the solutes, however, reach the root where they are utilized in the metabolism or are converted to insoluble storage products, thus keeping a lower osmotic concentration than the leaf cells. As a result of this difference in the osmotic concentration, therefore, solutes will always move from high to the low turgor pressure.

Perhaps the most convincing evidence in support of the mass flow theory has resulted from studies of the movement of extraneous substances in the phloem. It was observed that when viruses or growth substances were applied to illuminated leaves they were rapidly translocated out of the leaves together with the assimilate stream in the phloem (Benhett, 1937; Rohrbach and Rice, 1949). However when they are applied to shaded leaves, little or no translocation occurred. These observations strongly support the idea that the

sugars produced during photosynthesis in the leaves provided the turgor pressure gradients which are required for the operation of a mass flow. There is another explanation of the requirement for sugars, before translocation from the leaves can take place. If the process

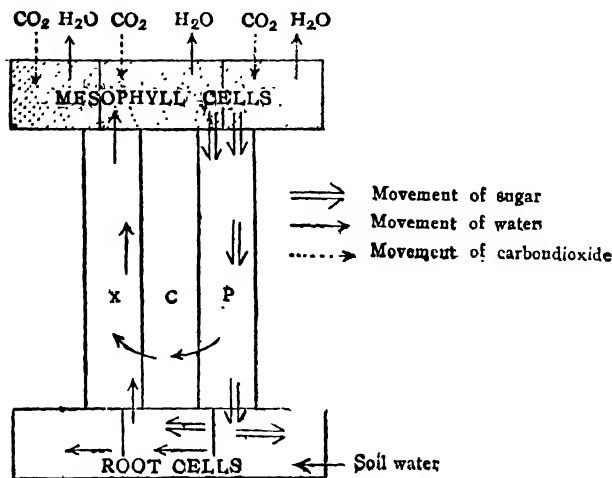


Fig. 14.4 Diagram illustrating the mechanism of solute translocation according to Münch hypothesis (modified after Crafts, 1931).

of translocation involves the expenditure of metabolic energy, then the energy might be provided in the form of ATP as a result of the metabolic breakdown of the sugars during respiration. The strongest evidence of the requirement of ATP has been provided by Rohrbach and Rice (1956). They showed that the translocation of ^{14}C labeled 2, 4 dichlorophenoxy acetic acid (2, 4-D) was severely reduced in plants which were deficient in phosphorus.

Electro-osmosis and mass flow theory: Two of the major objections to the Münch hypothesis are: (a) that it requires extensive turgor pressure to account for the flow through the pores of the sieve plates and (b) that it is essentially a non-physiological theory, while the phloem tissues themselves have a high physiological activity. Both of these objections have been answered by Spanner (1958) in his *electro-osmotic theory*. In this theory two types of mass flow was envisaged: a mechanical mass flow down the vacuole of the sieve element due to turgor gradient and an electrical or electro-osmotic mass flow through the pores of the sieve plates.

Spanner postulates that an electro-osmotic flow of water accompanied by solutes through the sieve pores is brought about by polarization of the sieve plates due to uptake of an ion on one side and release of the same ion on the other side of the plate. This unequal absorption and secretion of a charged ion would create an electric field

gradient which would produce an unidirectional flow through the sieve pores (Fig. 14.5).

While there is, as yet, no direct evidence for this theory but the work of Rohrbaugh and Rice (1958) apparently goes against Spanner's theory of electro-osmosis.

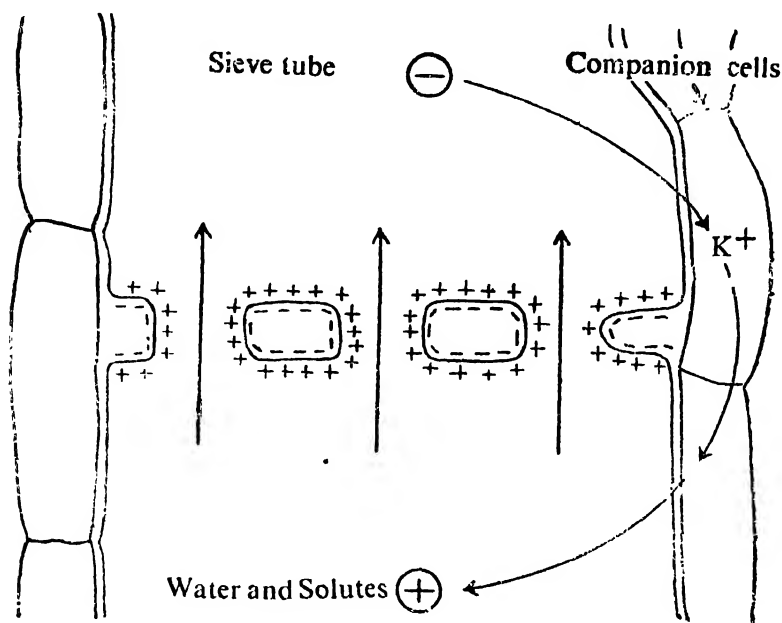


Fig. 14.5 Electro-osmotic flow of water and assimilates through the pores of sieve plate (modified after Spanner, 1958). Membrane potential is maintained by secretion of K^+ ions from companion cells.

Objections to the mass flow concept : Opponents of the mass flow hypothesis have raised a number of objections as to its validity for all tissues. The theory demanded that all cells which supplied solutes to the flow (source) must have a higher turgor pressure than the cells which are receiving the flow (sink). Several workers observed that this was not always so. For example, it was seen that tissues such as cotyledons, ageing leaves and senescing petals often exported food to more turgid growing or storage tissues.

Münch's original theory assumed that the sieve tubes were passive or dead and the protoplast played no part in the transport mechanism. Since then it has however been shown that the translocation is associated with the metabolic activity in the phloem. Thus, for example, in the absence of oxygen or in the presence of certain respiratory inhibitors like potassium cyanide (KCN) and 2, 4-dinitrophenol

(DNP), translocation of sugars is invariably reduced or stopped altogether. Furthermore if some type of electro-osmotic force is operative at the sieve plates, metabolic activity might be required for the circulation of the charged ion about the sieve pores.

A more serious objection to the mass flow theory resulted from the observation that the solutes could move simultaneously both upwards or downwards. Instances of simultaneous bidirectional movement was demonstrated separately by Palmquist (1939) and Chen (1951).

Studies on the simultaneous movement of different substances revealed that they do not move at the same rate. This goes against the mass flow theory. For example, Vernon and Aronoff (1952) supplied $^{14}\text{CO}_2$ to the leaves of soyabean plant and noted that the resulting radioactive sucrose had a higher rate of translocation in the phloem than the radioactive glucose and fructose which were also produced. Similar observations have been obtained by Biddulph and Cory (1957). Supporters of the mass flow idea have drawn as analogy of phloem transport with paper chromatography, where the solutes move as a bulk flow with the solvent in the paper but the different solutes undergo different degrees of absorption and retention by the paper.

14.3 Translocation of inorganic materials: In majority of plants the inorganic materials absorbed by the roots are translocated upwards through the xylem along with the transpiration stream. The term "inorganic materials" is loosely used as it includes the movement of the organic combination of some of the inorganic compounds (e.g. organic combination of N, S, P etc.) together with the inorganic constituents.

Use of radioactive isotopes showed that a trace of these inorganic salts may be used up in the adjacent tissues while moving upwards. The major part, however, moves to the leaf and is involved in the various metabolic reactions. Re-export of the material from the leaves in the phloem and again back to the roots has been observed during abscission.

That the xylem is the main site of transport has been observed by Phillis and Mason (1940) and others in their ringing experiments. More recently it has been supported by Stout and Hoagland who used radioactive isotopes to ascertain the path of mineral translocation and suggested that the translocation of mineral salts takes place through the xylem and at a relatively rapid rate.

The radio tracer study also shows the distribution of minerals in a various degree by Biddulph (1941). It has been experimentally proved that phosphorus and sulphur move very rapidly out of the leaf and move downwards in the phloem to the metabolically active zones. The movement of calcium shows a great contrast. After reaching the leaves through the xylem, it is never re-exported to the phloem but is utilized in the leaves.

14.4 Translocation between higher plants and their symbionts: Higher plants exhibit a variety of symbiotic association which may be mutualistic. One of the main features of a symbiotic association is the problem of translocation of substances. Smith, Muscatine and Lewis (1969) have demonstrated by means of ^{14}C that both the fungal parasites of the aerial part of plants or mycorrhizal fungi derive their carbohydrate from the host plant.

The fungal infection may markedly disrupt the normal pattern of translocation in the host plant. It has been shown by Livne and Daly (1966) that the normal bean plant exported about 50% of photosynthate whereas the leaves infected with fungus exported only 2%. These alterations are presumably brought about by the creation of a new "sink" in the vicinity of the fungal infection which maintain a concentration gradient between the host and the fungus.

Sucrose is mainly extracted by the fungus from the host and this sugar is rapidly converted to fungal carbohydrate such as trehalose, mannitol, various polyols and glycogen. These fungal carbohydrates are seldom translocated back to the host.

In case of parasites (e.g. *Cuscuta*, *Viscum album*, *Arceuthobium*) considerable movement of photosynthates occurs between host and parasites.

SELECTED QUESTIONS

1. Give an account of the translocation of the carbohydrate and nitrogenous compounds in and out of a storage organs.

For carbohydrate transport refer article 14.1 and for nitrogenous compound refer article 14.3

2. Give a detail account of the mechanism of phloem transport indicating critically the relative importance of the theories.

Refer article 14.2

3. "The evidence in favour of the pressure flow hypothesis do not necessarily plea it one a firm footing"—Discuss the validity of this statement.

Refer topic *mass flow hypothesis* in article 14.2.

4. Translocation of inorganic solutes from root to the leaf.

Refer article 14.3

5. What do you understand by translocation of solutes? Discuss its importance in the life of the plant.

Refer *introduction* of Chapte. 14 and articles 14.1 and 14.3

For the last part of the question add :

Translocation of solutes is a very important process in the life of a plant. The root system is responsible for the absorption of solutes from the soil whereas the leaves are mainly concerned with the synthesis of carbor compounds. Roots, however, cannot survive without the organic compounds synthesized in the leaves on the other hand also can not live without the solute absorbed by the roots. In order to maintain normal functioning of the plant these materials must transport from roots to the leaves and *vice versa*.

6. Give an account of translocation of organic substance and their storage in plants.

Refer articles 14.1 and 14.2

CHAPTER 15

Respiration

15.1 Definition : *From the thermo-dynamic stand point respiration is a process in which energy is liberated. From physico-chemical aspects, it is the oxidation of organic compounds, with molecular oxygen serving as an ultimate electron acceptor. This oxidation may be complete with the formation of carbon dioxide and water as the ultimate end products or it may be incomplete with the liberation of alcohol or other organic acids as the end products.*

Respiration does not mean a mere exchange of gases but the term is now employed to any process which is connected with the release of energy from the substances present in the cell. The energy that is liberated is stored in chemical form as ATP, liberated in the form of heat or it may be utilized in a variety of chemical reactions including protein and nucleic acid synthesis, cell-division, growth, movement, active transport of minerals etc. ATP is mainly produced in mitochondria as it is the main site of respiration but can be used both inside and outside these bodies.

The summary reaction for complete breakdown of 1 g molecule of hexose sugar with the liberation of energy is given below.



It means that 1 g molecule of hexose (180 g) on complete oxidation yields 673 Kgcals of energy or 1 g of hexose therefore yields 3.73 Kgcals of energy. Proteins and fats yield a larger amount of energy. Proteins on complete oxidation yield about 5.7 Kgcals per g of protein oxidised ; whereas fat yields on an average 9.1 Kgcals per g of fat oxidised.

Respiration is purely a catabolic phase of metabolism which involves the degradation of the chemical architecture of the complex organic molecules of cells. In this process, transfer of electrons from the organic molecules results in the reduction of oxygen to water and release their carbon as carbon dioxide. This continuous uptake of oxygen and release of carbon dioxide by plant cells was first demonstrated by de Saussure (1804).

Under anaerobic condition, however, carbon dioxide released in higher plants is very much similar to the carbon dioxide released from the process of fermentation e.g. alcoholic fermentation and lactic acid fermentation. The former, is found in yeast and clearly studied first by Pasteur in 1870, the latter occurs in mammalian muscle and studied in detail by Fletcher and Hopkins in 1907.

In both the processes hexose sugar is the starting point with the liberation of carbon dioxide and free energy from the system. The overall process can be written as follows :

Respiration



Fermentation

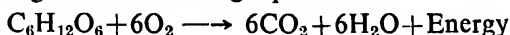


15.2 Types of respiration : There are mainly two types of respiration viz., (i) *aerobic respiration*—in which complete oxidation of respiratory substrate takes place in presence of oxygen resulting in the end products of carbon dioxide and water and (ii) *anaerobic respiration*—in which incomplete oxidation of respiratory substrate takes place in absence of external oxygen resulting in ethyl alcohol and carbon dioxide as the end products.

The energy released in the anaerobic respiration is very much less than that of aerobic respiration.

15.3 Respiratory quotient : *It is the ratio of the volume of carbon dioxide evolved to the volume of oxygen taken in the respiratory process which is represented by CO_2/O_2 and is written as RQ.*

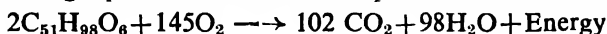
In general, when the complete oxidation of hexose sugar takes place according to the following equation



the respiratory quotient is unity i.e., $\frac{\text{CO}_2}{\text{O}_2} = \frac{6}{6} = 1$

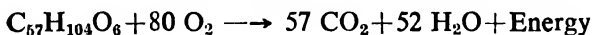
In other cases (e.g., proteins, fats or organic acids) respiratory quotient may vary from unit value, depending upon the nature of substrate and their oxidation.

(i) *Respiration of substances other than carbohydrates*—In case of *fats* the value of RQ falls as in fatty substances the proportion of oxygen to carbon is less than that in carbohydrate, hence larger amount of oxygen will be required for the oxidation of fats. The following equations show the complete oxidation of fats.



Tripalmitin

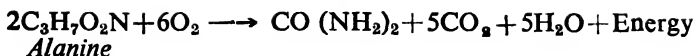
$$\text{RQ} = \frac{102}{145} = 0.7 \text{ i.e., less than unity.}$$



Triolein

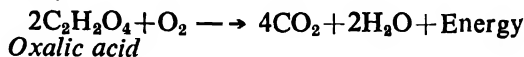
$$\text{RQ} = \frac{57}{80} = 0.7 \text{ i.e., less than unity.}$$

In case of *protein* the value of RQ is also less than 1, because proteins are made up of amino acids, which require more oxygen for complete combustion than carbohydrates do. The RQ of 0.8 is generally assigned to proteins.

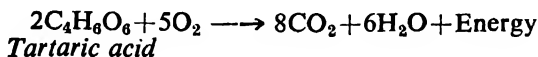


$$\text{RQ} = \frac{5}{6} = 0.83$$

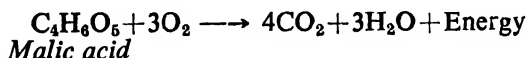
In case of *organic acids* which are rich in oxygen as compared with carbohydrates, little oxygen will be required for the oxidation process and consequently the value of RQ is greater than one. The following equations show the oxidation of organic acids and their subsequent RQ.



Here the RQ is $\frac{4}{1} = 4.0$ i.e., greater than unity.



$$\text{RQ} = \frac{8}{5} = 1.6$$



$$\text{RQ} = \frac{4}{3} = 1.3$$

(ii) *Incomplete oxidation of carbohydrates*—In many cases carbohydrates are not completely oxidised to carbon dioxide and water but an incomplete oxidation of sugars to organic acid takes place according to the following equation.



$$\text{RQ} = \frac{\text{CO}_2}{\text{O}_2} = \frac{0}{3} = 0$$

The synthesis of other organic acids in succulent plants takes place according to above scheme where there is utilization of oxygen without corresponding liberation of carbon dioxide and hence the RQ is less than one or even zero as no liberation of carbon dioxide has been observed in some of the cases.

(iii) *Utilization of oxygen without any corresponding liberation of carbon dioxide*—During maturation of fatty seeds, carbohydrate is converted to fat, when oxygen is released without any corresponding utilization of carbon dioxide. This serves as the internal supply in the process of respiration. So when such seeds respire, the volume of oxygen absorbed should have been more (as fat contains less oxygen); but since the oxygen liberated during conversion of sugar to fat serves as the source of oxygen, the actual intake of oxygen from atmosphere is less than the corresponding liberation of carbon dioxide and hence the RQ is more than one.

When, however, fatty seeds germinate, the process is just reverse and the RQ is less than unity as the conversion of fat to sugar is an oxygen consuming process without any liberation of carbon dioxide.

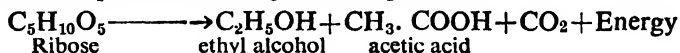
(iv) *Liberation of carbon dioxide without any utilization of oxygen*—At low oxygen concentration anaerobic breakdown of sugar will take place in addition to some aerobic process, which increases the amount of carbon dioxide and so incidentally raises the RQ to more than one. Similar condition prevails in the initial stage of germination of seeds whose coats are impermeable to oxygen (e.g., pea seeds). Major part of respiration by that type of seeds is anaerobic and so RQ is more than one.

During anaerobic respiration, carbon dioxide evolution takes place without oxygen uptake, giving an RQ of *infinity*; hence the simultaneous occurrence of aerobic and anaerobic respiration will give RQ's *above unity*.



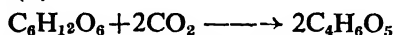
$$\text{RQ} = \frac{\text{CO}_2}{\text{O}_2} = \frac{2}{0} = \infty$$

Similarly fermentation of pentose sugars in actinomycetous fungus *Fusarium* takes place according to the equation.



Here also the RQ is infinity.

In the shoot of *Opuntia* and plants which show crassulacean acid metabolism (e.g. *Bryophyllum*) a large number of organic acids are formed due to fixation of carbon dioxide in the dark (for detail refer article 15.17 (ii)).



The resultant RQ is less than one.

James (1953) observed that under starved condition such as ageing green leaves, leaves in the dark or detached embryos exhibit RQ values consistently below unity.

In addition to the above, the persistence of detectable fermentation in senescent fruits even when these are in air, have usually the high RQ values. Temporary high RQ is observed during germination of some seeds in which the access to oxygen is limited by the tissues surrounding the embryo.

Significance of RQ : The principal significance of the study of RQ is to know the nature of the respiratory process. From the results of RQ the nature of the respiratory substrate that oxidised the transformation of the substrate and the bio-chemical mechanism of respiration can be determined. Thus, when the RQ is unity it indicates that the primary substrate is carbohydrate. When it is more than one some high oxygen containing substances like organic acids is found to be the respiratory substrate or it is found to result from

incomplete oxidation of a respiratory substrate which does not utilize much oxygen. In general, RQ less than one indicates that compounds other than carbohydrate are utilized or a carbohydrate is incompletely oxidised or formation of certain acids by succulent plants.

15.4 Pasteur effect and oxidative anabolism : When a tissue respiring anaerobically is subjected to aerobic condition by the addition of oxygen the anaerobic respiration stops abruptly and the rate of consumption of the respiratory substrate is reduced. This conversion of substrate is known as **Pasteur effect (PE)** after the observation of Pasteur. According to Dixon (1937) *the Pasteur effect is the action of oxygen in checking the high rate of loss of carbohydrate and in suppressing or diminishing the accumulation of the products of fermentation.*

The overall chemical reactions of both aerobic and anaerobic respiration suggest that the carbon dioxide evolved in aerobic respiration is three times greater than the amount produced under anaerobic respiration. But in many cases the actual ratio of carbon dioxide evolved is found to be less because the presence of oxygen lowers the rate at which sugar breakdown occurring in their absence.

Pasteur effect was first demonstrated by Pasteur while studying the alcoholic fermentation of yeast. Later on, such effect has been found to be operating in higher plants also, for example in the roots of carrot (Marsh and Goddard, 1932) ; barley leaves (James and Hora, 1940) ; rice (Taylor, 1942) ; potato tubers (Appleman and Brown, 1946) and in many others.

Blackman (1928), however felt that the carbon conservation by oxygen in the Pasteur effect was due to some synthetic reaction termed **oxidative anabolism (OA)**. According to Blackman resynthesis of the oxidative substance takes place due to transfer of carbon to the anabolic stream from an intermediate position of the catabolic stream (i.e. respiration). The assumption that the glycolytic products are anabolized back into carbohydrate or related compounds, suggests that the same carbon atoms may circulate through the system before their actual liberation as carbon dioxide. Blackman suggested that the oxygen had a three fold effect in respiratory metabolism ;

- (i) directly reacting in oxidation or more precisely in the reoxidation of reduced co-enzymes or electron carrier.
- (ii) in the resynthesis of glycolytic products.
- (iii) it increases indirectly the rate of glycolysis by "carbactivation".

But the concept of carbactivation gave an impetus to further investigation, whether or not to accept the hypothesis of oxidative anabolism.

This hypothesis of resynthesis of carbohydrate can not account for the Pasteur effect in yeast (Gottschalk, 1941). It, however, can not explain the similar phenomenon in higher plants.

The mechanism of Pasteur effect is still a matter of controversy. Many hypotheses have been put forward to account for the PE but all of them have failed to account fully for the phenomenon. However, it may be due to extra carbon dioxide in anaerobic respiration obtained by the degradation of substances other than carbohydrate, due to sudden blockage of glycolysis in presence of oxygen or it may be due to oxidative anabolism of the substances.

15.5 Fermentation: The phenomenon of fermentation is generally an oxidation process, characteristic of certain species of bacteria and fungi. Of all types of fermentation the best known is the *alcoholic fermentation*. Other examples of fermentation are butyric acid fermentation, lactic acid fermentation etc.

Although the process of alcoholic fermentation has been known from the very early period, the actual mechanism of this process was not known until 1860. During that period Gay-Lussac, however, demonstrated the formation of alcohol from sugar according to the overall chemical reaction; the stepwise degradation of the materials was however not known with certainty.



The reactions of most fermentation processes are anaerobic i.e. the reaction takes place in absence of oxygen, although there are some evidences of aerobic fermentation. In both the cases the end result is the incompletely oxidised compounds which accumulate within the tissues. Pasteur in 1857 suggested that alcoholic fermentation is an anaerobic process which is directly associated with the growth and metabolism of living matter.

After about 40 years in 1897, came Buchner's epoch making discovery that extract from yeast can rapidly ferment the sugar solution. Buchner's work led the later workers to study the properties of yeast juice more intensively and in 1905 Harden and Young demonstrated by dialysing the material that an active principle known as "*zymase*" was present in the yeast which brought about the reaction.

Mechanism of alcoholic fermentation—It is evident from the above equation that two molecules of alcohol and two molecules of carbon dioxide together with certain amount of energy result from the breakdown of a molecule of sugar in alcoholic fermentation. The reactions as shown above occurs through a number of steps or pathways¹ and several intermediate products are formed. Alcoholic fermentation takes place in absence of atmospheric oxygen i.e., it is an anaerobic process.

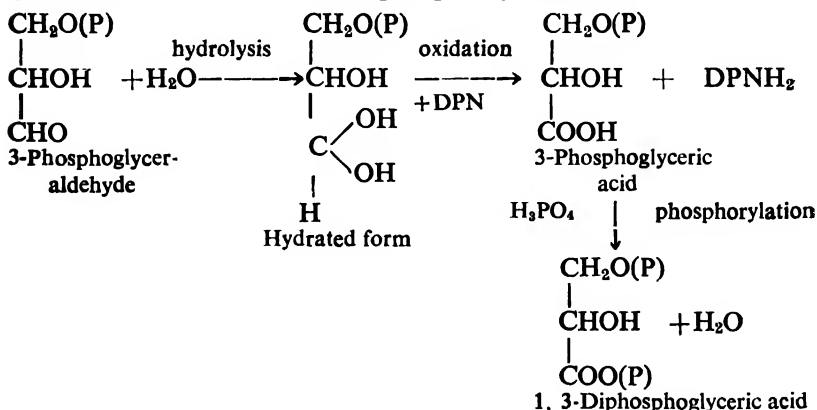
The first stage in the process of fermentation is the phosphorylation of hexose with the ATP molecules. This change takes place in three steps. The first step is the transfer of one of the phosphate

¹ The pathway of alcoholic fermentation i.e. glycolytic pathway is also known as **EMP pathway** or Embden-Meyerhof-Parnas pathway.

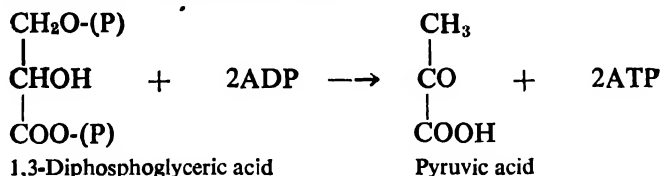
groups of ATP to glucose to form glucose 6-phosphate and ADP with the help of enzyme *hexokinase*. Glucose 6-phosphate then undergoes an isomeric change to fructose 6-phosphate. In the third step the phosphate molecule from another molecule of ATP unites with the fructose 6-phosphate to form fructose 1, 6-diphosphate.

Fructose 1, 6-diphosphate then breaks into two equal parts—3-phosphoglyceraldehyde and dihydroxyacetone phosphate.

3-phosphoglyceraldehyde then by hydrolysis, oxidation and phosphorylation gives rise to 1, 3-diphosphoglyceric acid.



1,3-Diphosphoglyceric acid is then involved in the transfer of 2 phosphate groups to ADP with the formation of corresponding ATP molecules and the pyruvic acid.



So, for a complete breakdown of a molecule of glucose, four ATP molecules will be produced and since two molecules of ATP were utilized in the initial stages of reaction, so that the net gain of ATP molecule upto formation of pyruvic acid is two molecules. If one such high energy phosphate bond represents 11-12 Kcal of energy then the energy released upto this change is 22-24 Kcal

Since in one of the stages of oxidation of 3-phosphoglyceraldehyde DPN is reduced to DPNH_2 , there must be a continuous supply of DPN in order to continue the process, otherwise the process will come to a standstill. In the process DPNH_2 must be reoxidised to DPN, which will again be used in the reaction. This reoxidation of DPNH_2 takes place in the subsequent reactions during reduction of pyruvic acid.

The immediate fate of pyruvic acid is decarboxylation by the enzyme *carboxylase* to form acetaldehyde and carbon dioxide.

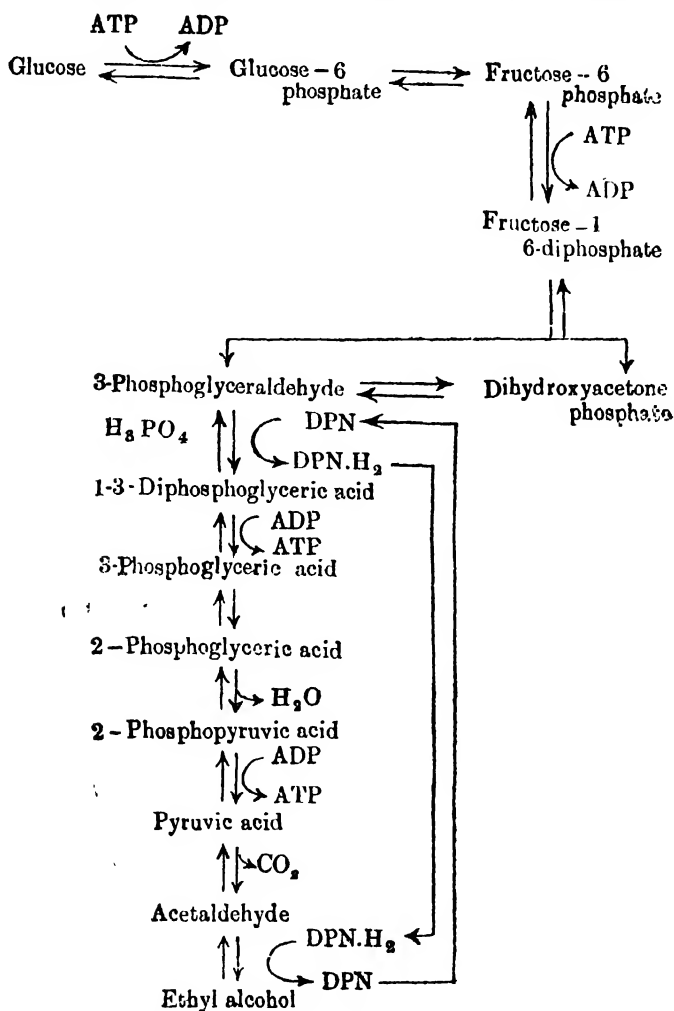
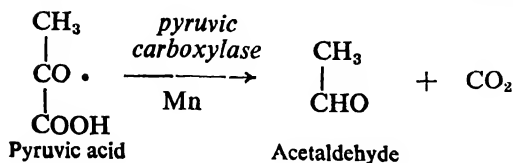
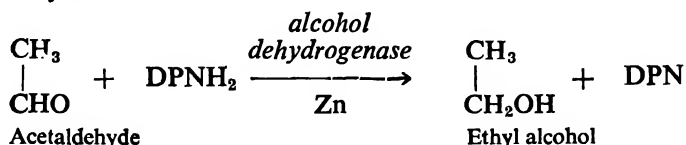


Fig. 15.1 Summary of the reactions in alcoholic fermentation.



In the final stage, acetaldehyde is reduced to alcohol by the hydrogen derived from the DPNH_2 formed during oxidation of 3-phosphoglyceraldehyde.



The summary reactions of alcoholic fermentation are given in Fig. 15.1.

15.6 Chemical pathway of respiration (Mechanism of respiration) :

The exact sequence of chemical reactions involved in the process of respiration is an outstanding feature. The enzymes which are responsible for these biochemical changes have also been studied in details. The pioneer worker on the biochemistry of respiration was Buchner (1897) who first demonstrated the conversion of sugar to alcohol and carbon dioxide by the active yeast juice during fermentation. This has been developed further by Palladin (1922) and Kostychev (1927) who demonstrated the occurrence of the enzymes responsible for fermentation in higher plants. Their work in this line also support the vital aspect of respiration.

The critical study of the process of respiration as it proceeds in the living cell, indicates that there are two important phases (i) the oxidation of respiratory substrate (carbohydrate) to pyruvic acid known as *glycolysis* and (ii) the subsequent oxidation of pyruvic acid.

The first phase takes place either in presence or in absence of oxygen but the second phase depends on the nature of tissues and availability of oxygen. If atmospheric oxygen is available aerobic oxidation of pyruvic acid takes place, if oxygen is not available incomplete oxidation of pyruvic acid takes place.

(i) Oxidation of respiratory substrate to pyruvic acid or glycolysis :

The fundamental mechanism of oxidation-reduction and phosphorylation which are the main steps of glycolysis proceeds in the same way as in alcoholic fermentation (refer article 15.5).

The first stage of glycolysis is the phosphorylation of hexose sugar (glucose) to form glucose 6-phosphate. Synthesis of glucose 6-phosphate is brought about by the transfer of a phosphate group from ATP to glucose, as a result glucose 6-phosphate and ADP are formed. It is catalysed by the enzyme *hexokinase*. Glucose 6-phosphate is then converted into fructose 6-phosphate by the enzyme *phosphohexo isomerase*. Fructose 6-phosphate can also be formed from fructose and ATP in the same manner in which glucose 6-phosphate is formed. It is further converted to fructose 1,6-di-phosphate when the former reacts with ATP transferring the phosphate

group from ATP to fructose 6-phosphate. This reaction is catalysed by the enzyme *phosphohexokinase*.

The enzyme *aldolase* then splits fructose 1, 6-diphosphate equally into two halves to yield two triose phosphates (3-phosphoglyceraldehyde and dihydroxyacetone phosphate). These two isomeric triose phosphates are interconvertible by means of second isomeric enzyme *triose phosphate isomerase*. Of these two triose phosphates 3-phosphoglyceraldehyde then directly enters into the respiratory process and is converted to 1, 3-diphosphoglyceric acid by the enzyme *dehydrogenase*, inorganic phosphate and hydrogen acceptor (DPN).

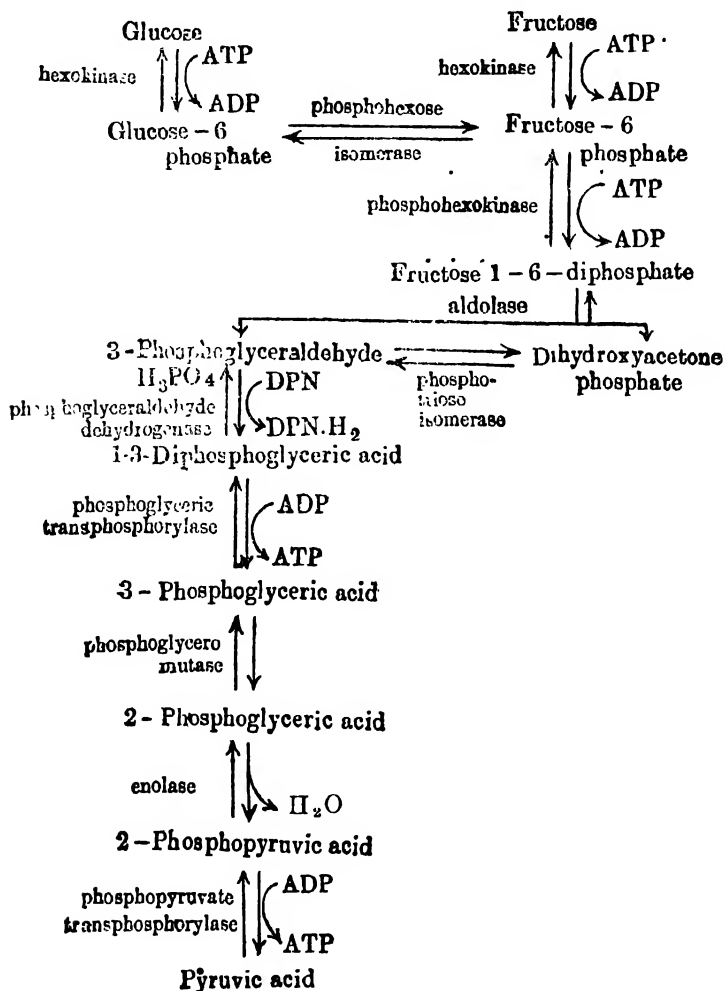
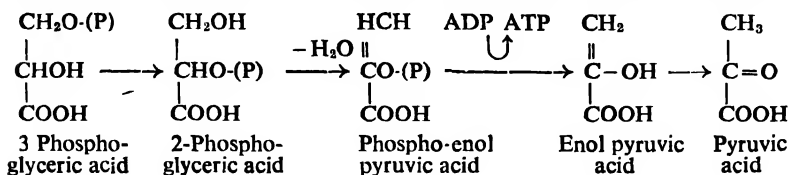


Fig. 15.2 Summary of the glycolytic process in respiration.

1-3 diphosphoglyceric acid then reacts with the enzyme *transferase* or *kinase* to produce 3-phosphoglyceric acid (PGA). The phosphate group being removed from the substrate and attached to ADP to form a new ATP molecule. 3-PGA then changes to 2-PGA by simply changing the position of phosphate group from 3rd carbon position to 2nd carbon of the glyceric acid with the help of the enzyme



phosphoglyceromutase.¹ 2-Phosphoglyceric acid (2-PGA) is then converted to 2-phosphopyruvic acid with the release of a molecule of water by the enzyme *enolase*. 2-phosphopyruvic acid then releases its phosphate group to ADP and converts the substrate into pyruvic acid and a molecule of ATP by the enzyme *transferase*. The whole sequence of the chemical reactions is diagrammatically shown in Fig. 15.2.

Pyruvic acid is one of the key intermediates in the process of respiration. Further oxidation of pyruvic acid depends upon the supply of oxygen; if oxygen is present aerobic oxidation of pyruvic acid takes place, while in absence of oxygen anaerobic oxidation of pyruvic acid results.

(ii) *Aerobic oxidation of pyruvic acid*: When there is a free supply of oxygen, majority of plant tissues oxidise pyruvic acid to carbon dioxide and water. This oxidation takes place in a series of reactions which proceed through a cycle known as *citric acid cycle*, *tricarboxylic acid cycle* (or *TCA cycle*) or better known as *Krebs cycle*, after H. A. Krebs (1937) who first proposed and formulated the mechanism. Through the Krebs cycle and *electron transport system*, the pyruvic acid is oxidised to carbon dioxide and water and through its association with the electron transport system 30 ATP molecules are formed. Krebs cycle is therefore more efficient in the release of energy than glycolysis or fermentation.

The initial stage of oxidation of pyruvic acid is the removal of carbon dioxide (decarboxylation) and is very much similar to the initial reaction of pyruvic acid breakdown occurring during alcoholic fermentation. Although the details of reactions are still a biochemical puzzle but that acetyl co-enzyme A (acetyl Co-A) is the key product has been demonstrated by Lynen (1951). The first step of this process is the decarboxylation of pyruvic acid to form an 'active' aldehyde

¹ Mutases catalyze the transfer of phosphate group at a low energy level from one position on a carbohydrate to another position on the same molecule. This enzyme requires Mg^{++} for its activity.

reacting with the co-enzyme thiamine pyrophosphate (TPP). The two carbon aldehyde is active in the sense that unlike anaerobic oxidation here it is attached with this co-enzyme. This activated aldehyde now reacts with the second co-enzyme, lipoic acid. The disulphide group (S-S) of the acid is reduced by the activated aldehyde to form an -SH group and acetyl lipoic acid. Thiamine pyrophosphate is released in the reaction. This 2 carbon unit now reacts with the co-enzyme A (SH.Co-A) to form a completely reduced

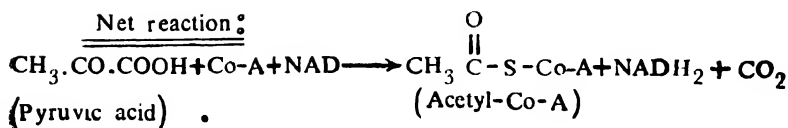
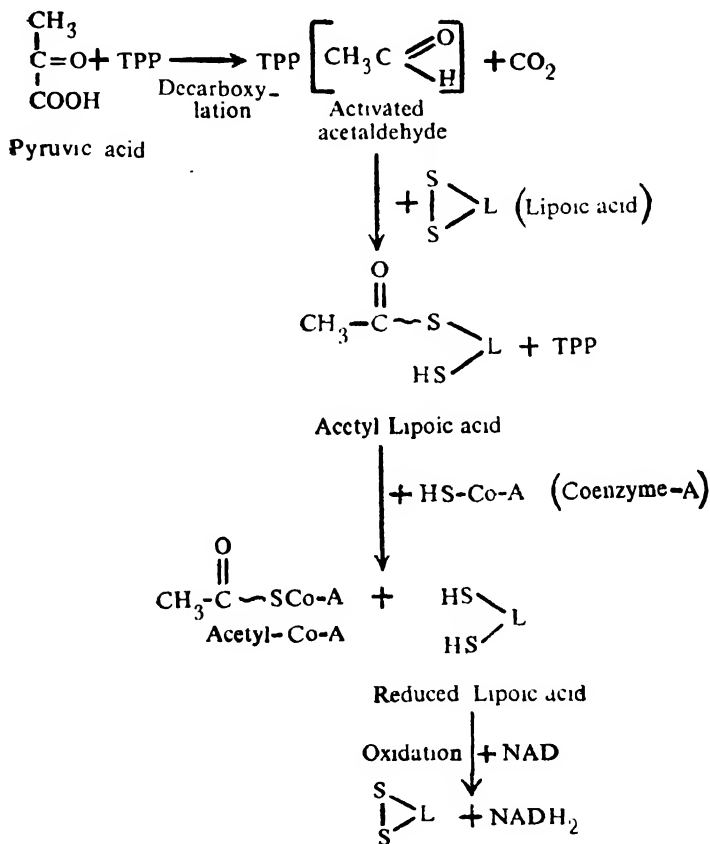
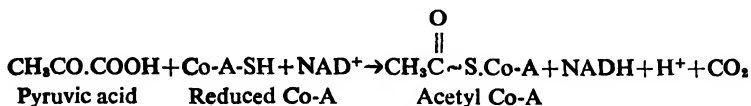


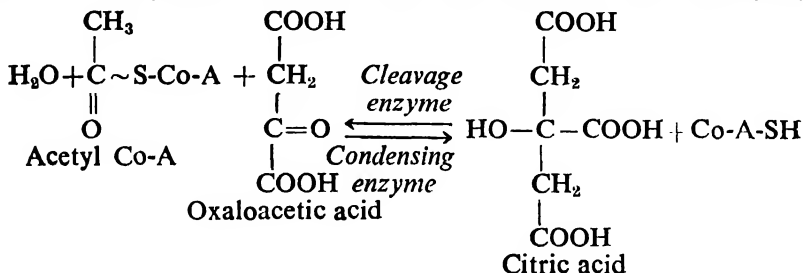
Fig. 15.3 Oxidative decarboxylation of pyruvic acid.

lipoic acid and acetyl co-enzyme A. This reduced lipoic acid now reacts with NAD^+ to give rise to reduced NAD^+ and the original lipoic acid. The whole scheme of this oxidative decarboxylation is outlined in Fig. 15.3. The net reaction of the oxidative decarboxylation is given below :



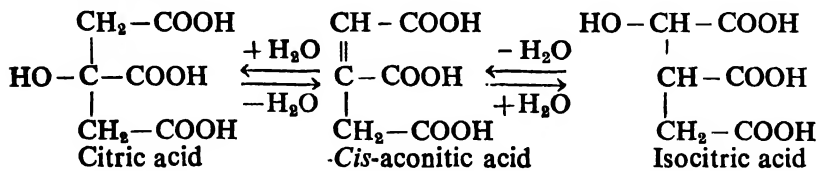
The acetyl Co-A then unites with the organic acid and in presence of oxygen the whole reaction goes to completion and liberates large amount of energy which is conserved as ATP.

This cycle is initiated by the condensation of acetyl Co-A and oxaloacetic acid to form citric acid, catalyzed by *condensing enzymes* (as the first product is citric acid hence the name *citric acid cycle*).



Citric acid is a six carbon compound and incidentally contains three carboxyl groups (hence also named as *tricarboxylic acid cycle*). Then there is a rearrangement of the citric acid molecule by the removal and addition of a molecule of water to form isocitric acid via *cis*-aconitic acid—all of these reactions are catalysed by the enzyme *aconitase* which require Fe^{++} . First of all, it involves a hydration of citric acid to give rise to *cis*-aconitic acid and in the second stage *cis*-aconitic acid further gives rise to isocitric acid.

The formation of *cis*-aconitic acid from citric acid is due to asymmetric dehydration and the formation of isocitric acid from *cis*-aconitic acid is the result of stereospecific hydration—both these processes are catalysed by a single enzyme *aconitase*. Fe^{++} is required in the process.



Isocitric acid is oxidised to form a keto acid, oxalosuccinic acid in the presence of *isocitric dehydrogenase* and NADP^+ . It is incidentally

the first oxidation step in the Krebs cycle, where two electrons and two hydrogen ions (H^+) being removed from the substrate and

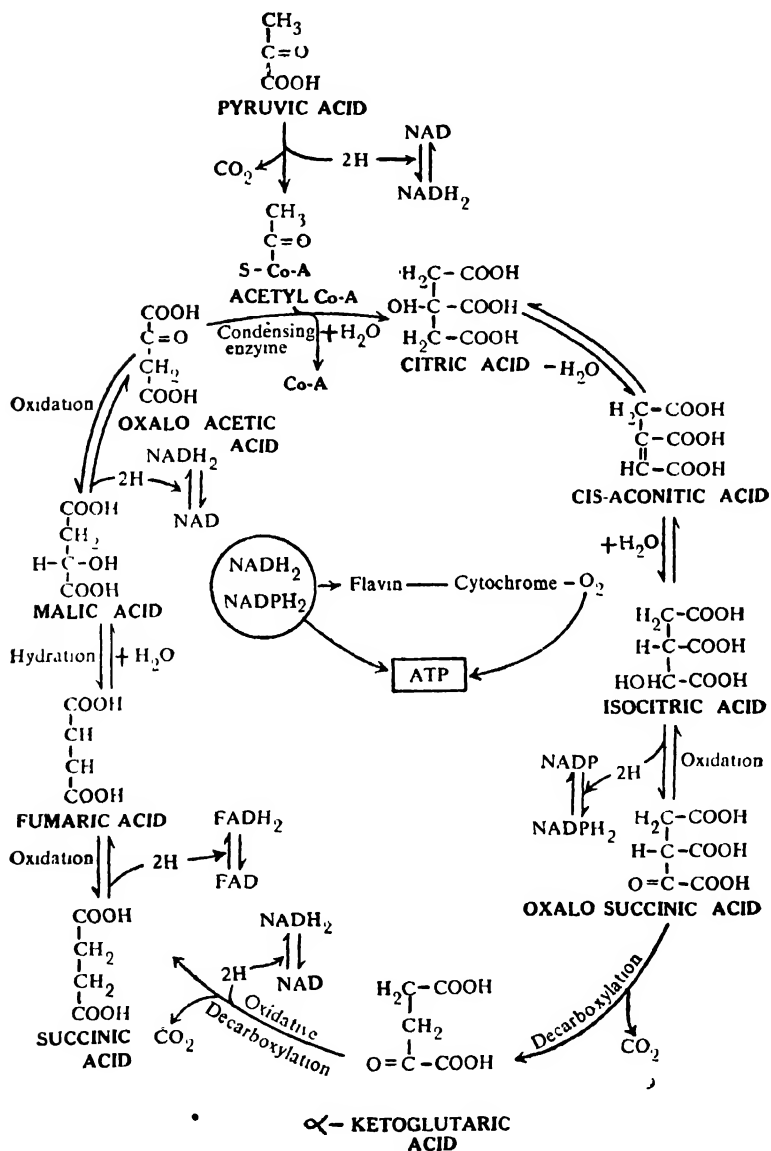
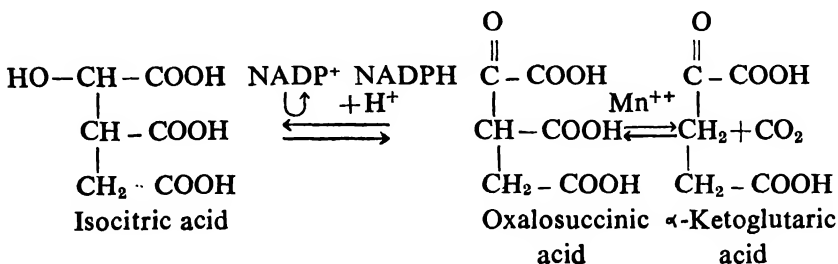


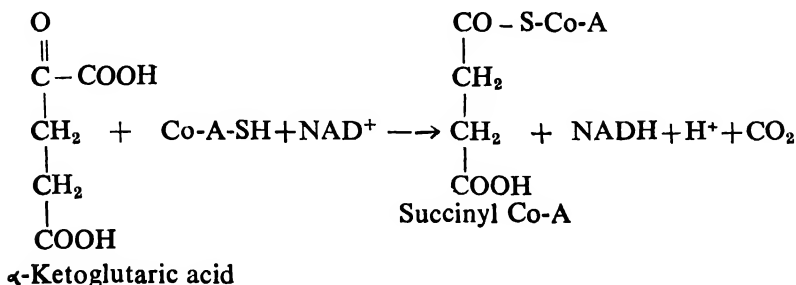
Fig. 15.4 Krebs cycle.

these are ultimately being taken up by the co-enzyme NADP^+ to form $\text{NADPH} + \text{H}^+$. Further, oxalosuccinic acid by decarboxylation yields the most important keto acid in the plant, α -ketoglutaric acid. Manganese (Mn^{++}) is required for the decarboxylation reaction.

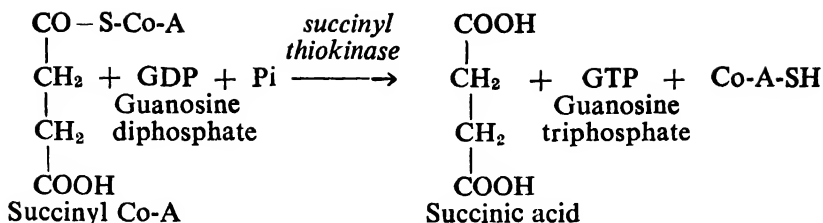
Oxalosuccinic acid which is formed is firmly bound to the surface of the enzyme and is not released as a free intermediate in either the oxidative decarboxylation of isocitrate or the reverse reaction, the reductive carboxylation of α -ketoglutaric acid.



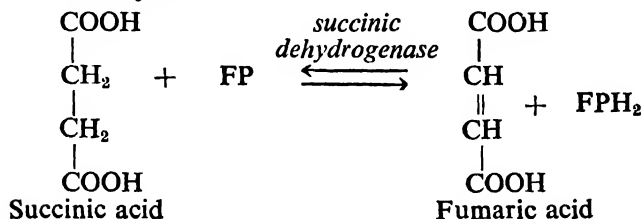
α -Ketoglutaric acid then by oxidative decarboxylation is converted to succinic acid. The oxidation of α -ketoglutaric acid is very much analogous to that of pyruvic acid and in that reaction thiamine pyrophosphate (TPP) is involved in the decarboxylation of α -ketoglutaric acid. The TPP-complex then reacts with oxidised lipoic acid to form succinic semialdehyde. Succinic semialdehyde then reacts with Co-A to form succinyl Co-A and reduced lipoic acid. Reduced lipoic acid then is reoxidised by a NAD-containing enzyme, where NAD^+ is reduced to $\text{NADH} + \text{H}^+$. The whole enzyme complex catalysing these reactions is termed as *α -ketoglutaric dehydrogenase*. Last stage of this reaction is the conversion of succinyl Co-A to succinic acid.



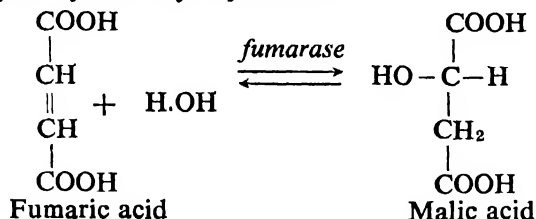
It is the second oxidation step where the energy locked in succinyl Co-A is released and utilized in the formation of an energy rich pyrophosphate bond. Thus in this conversion there is a side chain where guanosine diphosphate (GDP) and inorganic phosphate unites to yield a molecule of guanosine triphosphate (GTP).



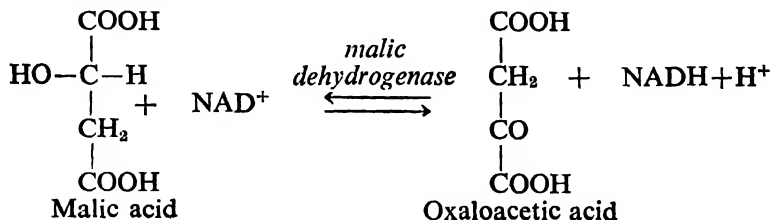
Succinic acid then by the release of two electrons and two hydrogen ions (H^+) is converted to fumaric acid. It is the only reaction in the Krebs cycle where these hydrogen are taken by ferriflavoprotein and not by any pyridine nucleotide. The enzyme catalysing this reaction is *succinic dehydrogenase*. It is the third oxidation step of the Krebs cycle.



The formation of malic acid from fumaric acid occurs as a result of the addition of water at the double bond of fumaric acid and is catalysed by the enzyme *fumarase*.



The last step is another oxidation process where malic acid is oxidised to oxaloacetic acid by the enzyme *malic dehydrogenase*. Here NAD^+ is reduced to $\text{NADH} + \text{H}^+$.



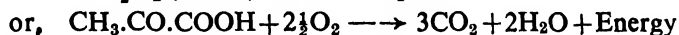
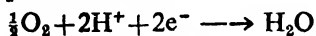
This reaction completes the cycle, forming oxaloacetic acid which then may continue in the cycle by reacting with acetyl Co-A to form citric acid again.

All the reactions of Krebs cycle are reversible except the oxidative decarboxylation of α -ketoglutaric acid. As pointed out earlier that this reaction is entirely analogous to the irreversible oxidative decarboxylation of pyruvic acid. This means that the cycle cannot be made to proceed in a reverse direction although individual sections are reversible (i.e. from oxaloacetic acid to succinic acid or from α -ketoglutaric acid to citric acid). Similarly acetyl Co-A and CO_2 cannot be converted to pyruvic acid by a reverse reaction.

It is very important to consider the stoichiometry of these reactions in details. Starting with a molecule of pyruvic acid and tracing its oxidation to acetyl Co-A and the subsequent oxidation of the thioester through one turn of the Krebs cycle, the following reactions are involved :

(a) There are five oxidation steps (e.g. pyruvic acid to acetyl Co-A, isocitric acid to oxalosuccinic acid, α -ketoglutaric acid to succinic acid, succinic acid to fumaric acid and malic acid to oxaloacetic acid). In each of these reactions 2 electrons are removed from the substrate ; the subsequent reduction of O_2 by these electron pairs results in the utilization of five atoms or $2\frac{1}{2}$ molecules of O_2 .

(b) When the five pairs of electrons are used to reduce oxygen, 5 molecules of H_2O are formed.



2 molecules are utilized directly in the cycle. To account for the net production of 2 molecules of H_2O in the cycle, a third molecule of H_2O must be accounted for. This may be done by realizing that in the *succinyl thiokinase* reaction, a thioester has been hydrolyzed without the consumption of a molecule of H_2O . This is due to the fact that the elements of H_2O have been produced by the conversion of GDP and H_3PO_4 (Pi) to GTP in the same reaction.

(c) Finally, 3 molecules of CO_2 , representing the equivalent of the 3 carbon atoms of pyruvic acid are released in the reactions

Since oxidation of a molecule of glucose yields two molecules of pyruvic acid, so the complete oxidation of a molecule of glucose requires five molecules of oxygen and liberates six molecules of carbon dioxide and four molecules of water. But as the overall reaction of respiration shows the requirement of six molecules of oxygen for oxidation, the remaining one molecule of oxygen is utilized in converting, DPNH_2 to DPN (in the glycolytic stage) in order to get a continuous supply of DPN to run the reactions. The other two molecules of water liberated are from the glycolytic stage.

(iii) *Anaerobic oxidation of pyruvic acid* : Anaerobic oxidation of pyruvic acid generally takes place when oxygen is not available and unfavourable conditions prevail. The products of anaerobic respiration are generally incompletely oxidised compounds like organic acids or alcohols together with carbon dioxide. This alcohol is mostly

ethyl alcohol in case of some higher plants and in some lower groups of plants (e.g., yeasts and some fungi).

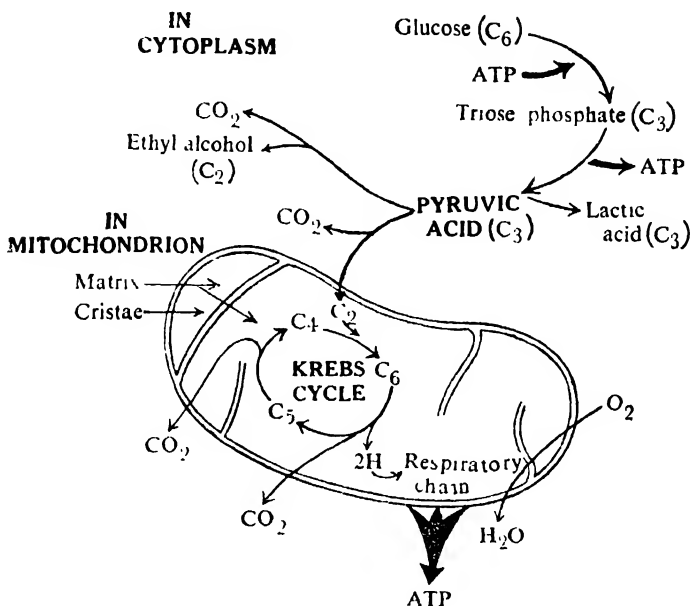
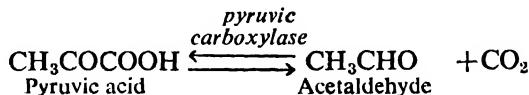
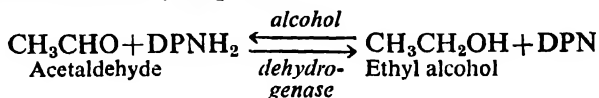


Fig. 15.5 Location within the cell of the major reactions involved in the complete degradation of glucose.

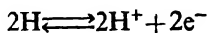
At first decarboxylation of pyruvic acid under the influence of the enzyme *pyruvic carboxylase* results into the production of acetaldehyde and carbon dioxide.



This carbon dioxide liberated as one of the end products. Acetaldehyde thus formed is then converted into ethyl alcohol by the action of the co-enzyme DPNH_2 (produced in the glycolytic phase) and the enzyme is *alcohol dehydrogenase*.



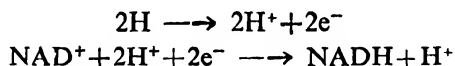
Electron transport system—Due to intramolecular alterations in five substrates of Krebs cycle, a pair of hydrogen atoms (2H) is being removed. Since the hydrogen atom can dissociate into two protons and two electrons



the oxidation process of these five stages is equated to the removal and transport of electrons to molecular oxygen.

The pair of hydrogen atoms ($2\text{H}^+ + 2\text{e}^-$) removed in the oxidation steps of Krebs cycle do not combine directly with molecular oxygen but rather, they are transported through an *electron transport system* or through an *respiratory chain*. Through this system the reduced co-enzymes like NADP^+ , NAD^+ and FAD which are formed in Krebs cycle are reoxidised. The co-enzymes in this chain successively undergo reduction and oxidation by accepting hydrogen or electrons from the preceding member of this chain and passing it to the next member of the chain. The energy released in this oxidation is utilized in the synthesis of ATP.

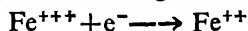
The electron transport system is strictly a sequential series of cytochrome enzymes, capable of passing electrons from one to another. The hydrogen pairs released in the oxidation steps of Krebs cycle end up ultimately in combination with the co-enzyme *nicotinamide adenine dinucleotide* (NAD^+). Of these two protons and two electrons, one proton and two electrons are transferred to the co-enzyme with an extra proton being released in the medium as a H^+ ion.



These reduced NAD^+ then become reoxidised by another co-enzyme *flavin adenine dinucleotide* (FAD). Two electrons and one proton from NADH are now transferred to FAD group. Thus the reduction of FAD takes place according to



Reduced co-enzymes then transfer a pair of electrons to the communal chain of cytochromes and release 2H^+ into the medium. It is in this respiratory chain a complete exchange of 2H for $2\text{H}^+ + 2\text{e}^-$ occurs. Electrons are passed through the cytochromes b , c_1 , c , a and a_3 , one at a time and ultimately to molecular oxygen. The whole scheme of the electron transport system is given below. In this system hydrogen ions are released at the time of reoxidation of co-enzyme Q only the electrons are passed through the cytochromes. Now since the cytochrome has a *heme* prosthetic group, its iron atom is reduced and oxidised by accepting and donating one electron.



In this way the electron is passed from one cytochrome to another and ultimately to the terminal end, molecular oxygen picks up this electron and forms water with hydrogen ions of the cytoplasm.

Somewhere along this chain, probably between flavin and cytochrome b , is involved a newly discovered carrier, co-enzyme Q_{10} , a quinone chemically related to vitamin K .

In the transfer of electrons from the substrate to molecular oxygen, electrons drop from a higher potential energy to a lower potential energy represented by the formation of water. As the electrons are passed down from one carrier to the next, they release a part of their energy at each oxidation-reduction step. This energy is now coupled with the union of ADP and inorganic phosphate to synthesize ATP. Thus the synthesis of ATP through this coupling system or

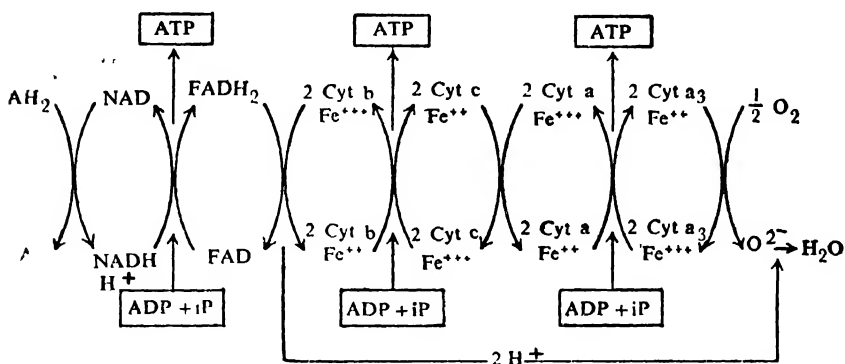
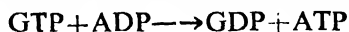


Fig. 15.6 Electron transport system.

electron transport system is called *oxidative phosphorylation*. The synthesis of ATP takes place in the oxidation of $NADH$, cytochrome b and cytochrome a (refer Fig. 15.5).

The oxidation of a molecule of pyruvic acid to carbon dioxide and water is accompanied by the formation of 15 molecules of ATP. Since in the Krebs cycle pyruvic acid, isocitric acid, α -ketoglutaric acid and malic acid, reduces a molecule of NAD^+ and in the electron transport chain 3 ATP molecules are synthesized in their complete turn of a cycle. So a total of $3 \times 4 = 12$ ATP molecules are synthesized. Oxidation of succinic acid to fumaric acid yields 2 ATP molecules as the chain starts from FAD . One ATP molecule is generated in the conversion of succinyl Co-A to succinic acid via GTP according to



This yields a total of 15 ATP or $15 \times 2 = 30$ ATP for the oxidation of 2 molecules of pyruvic acid derived from a molecule of glucose.

In the initial stage of glycolysis the conversion of 3-phosphoglyceraldehyde to 1-3-diphosphoglyceric acid is an oxidation process which results in the formation of $NADH$. In aerobic respiration, another electron transport chain occurs to form 3 molecules of ATP. So, a total of 6 molecules of ATP will be formed during this oxidation. This is a case of *substrate phosphorylation*, as the production of ATP takes place by the direct oxidation of the substrate.

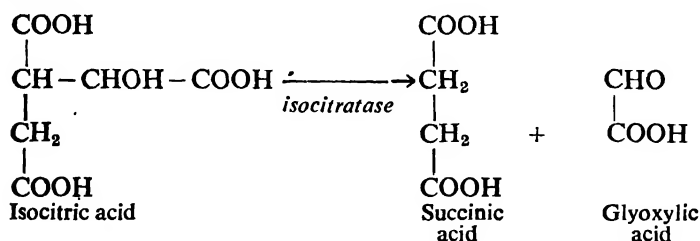
As it is evident from previous discussion that glycolysis yields a net gain of 2 ATP molecules, thus it will bring the total of 38 ATP molecules for the complete oxidation of glucose.

It is clear from the above discussion that when the pyruvic acid, isocitric acid and malic acid are oxidised, 3 ATP molecules are liberated per atom of oxygen reduced. In case of oxidation of α -ketoglutaric acid 4 ATP molecules are liberated, whereas when succinic acid is oxidised 2 ATP molecules are formed per atom of oxygen reduced. Thus the ratio of moles of inorganic phosphate esterified to form ATP per atom of oxygen consumed during the oxidation process is called P/O ratio. It is really a measure of energy yield from the oxidation of the substrate. In case of α -ketoglutaric acid the P/O ratio is 4, whereas with malic acid, pyruvic acid and isocitric acid the ratio is 3 and with succinic acid it is 2.

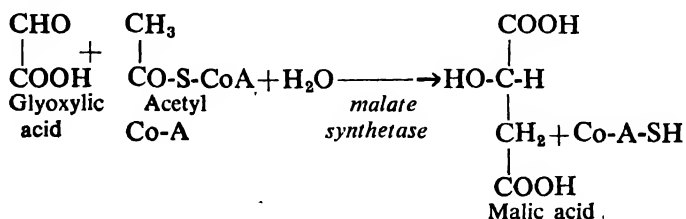
15.7 The glyoxylic acid cycle : A modified Krebs cycle : In some plants and micro organisms (e.g. yeasts, molds and bacteria), a variation of Krebs cycle exists whereby succinic acid, malic acid and oxaloacetic acid are synthesized from acetyl-CoA. This results in a net synthesis of the dicarboxylic acid, oxaloacetic acid, which is an acceptor molecule of acetyl-CoA in the Krebs cycle (Fig. 15.7).

The two reactions are important in the glyoxylic acid cycle and these results in

(i) Splitting of isocitric acid to succinic acid and glyoxylic acid bypassing the α -ketoglutaric acid.



(ii) The condensation of glyoxylic acid with acetyl-CoA resulting in the formation of malic acid



Thus oxaloacetic acid can be regenerated both from succinic acid via the Krebs cycle and from glyoxylic acid by condensation

with acetyl-CoA. Two molecules of active acetyl Co-A are converted in this cycle,

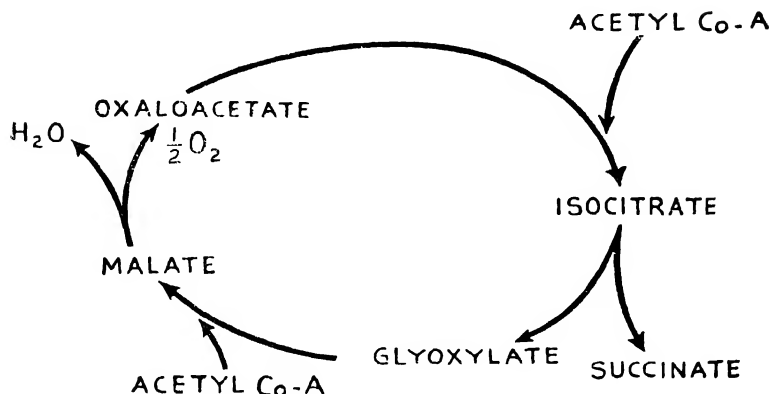
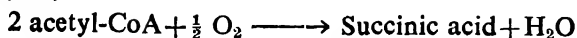


Fig. 15.7 The glyoxylic acid cycle.

15.8 Pentose phosphate pathway or direct oxidation pathway : For the last 30 years when the concept of breakdown of carbohydrate to carbon dioxide and water through glycolytic pathway followed by the Krebs cycle is based, there is an accumulation of belief that the aerobic oxidation of carbohydrate may not produced in the same way as has been indicated earlier. According to the classical view, the degradation of carbohydrate upto pyruvic acid takes place in the same way both in aerobic and anaerobic process, after which the path diverge leading to complete breakdown of carbohydrate to carbon dioxide and water as well as to the alcoholic fermentation.

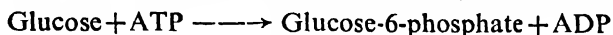
According to Warburg *et al* (1935), Dickens (1938) and others the divergence of chemical reactions in these two processes (aerobic and fermentation) takes place early in the reaction and even before the glycolytic pathway. This diverse pathway is known variously as "Warburg-Lipmann-Dickens pathway", "direct oxidation pathway" or more commonly as pentose phosphate pathway.

The existence of this type of reactions was indicated by the fact that in same tissues the classical inhibitors of glycolysis e.g. iodoacetate and fluoride, had no effect on the utilization of glucose. Further the experiments of Warburg, resulting in the discovery of NADP^+ and the oxidation of glucose-6-P to 6-phosphogluconic acid, led the glucose molecule into an unfamiliar area of metabolism. Moreover, experiments with ^{14}C by labelling glucose in the C-1 position indicate their rapid utilization than was glucose labelled in the C-6 position. If the glycolytic sequence were the only means whereby glucose

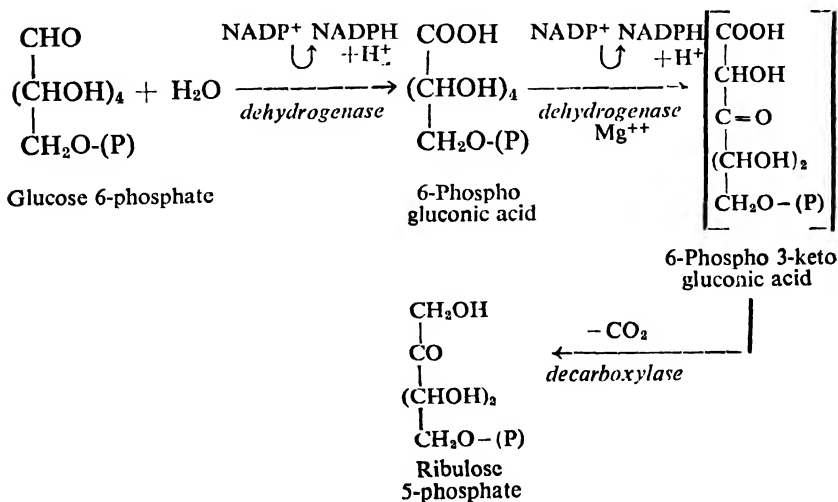
could be converted to pyruvic acid and subsequently broken to CO_2 , then $^{14}\text{CO}_2$ should have been produced at an equal rate from glucose-1- C^{14} and glucose-6- C^{14} . These observations stimulated work and the work has resulted in the delineation of pentose phosphate pathway.

According to this cycle, for every six molecules of hexose sugar involved, one molecule is actually oxidised to carbon dioxide and water with the re-synthesis of five molecules of hexose. Although this cycle is found to be independent of glycolysis, but the existence of common intermediates suggests the possible linkage between the two. This cycle differs from the glycolytic cycle in that it is dependent on NADP^+ and insensitive to certain chemicals which inhibit glycolysis.

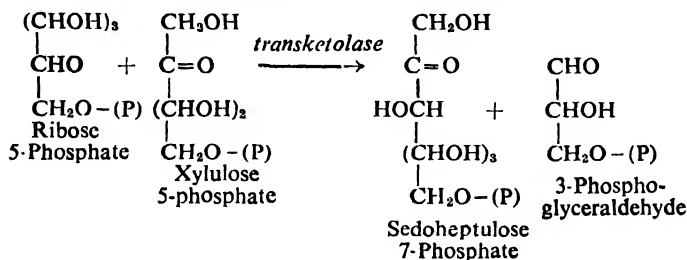
This cycle (Fig. 15.8) provides an alternative way for the oxidation of glucose to phospho-glyceraldehyde. The first stage of this cycle is same as the glycolytic pathway where there is a phosphorylation of glucose to glucose 6-phosphate by ATP and enzyme *hexokinase*.



Glucose 6-phosphate is oxidised to 6-phosphogluconic acid utilizing NADP^+ (as hydrogen acceptor) and water. 6-phosphogluconic acid is then oxidised in presence of co-enzyme NADP^+ to form NADPH and 3-keto, 6-phosphogluconic acid which is decarboxylated to form ribulose 5-phosphate and carbon dioxide. Because the reactions involves both oxidation and decarboxylation, it was first suggested that 3-keto, 6-phosphogluconic acid might be an intermediate product prior to decarboxylation. No direct evidence in support of such a compound has been offered and the reaction is believed to be a single-step oxidative decarboxylation resulting in the formation of ribulose-5 phosphate.



Ribulose 5-phosphate is then converted to other pentoses either ribose 5-phosphate or xylulose 5-phosphate by *phosphoribo isomerase* and *phosphoketopentose epimerase* respectively. All these three pentoses, ribose, ribulose and xylulose enter into a series of reactions with the formation of triose phosphate with the enzymes *transketolase*, *transaldolase* and *aldolase*. Although the details of their formation is not known, but possibly it is formed by a reverse pathway of that of photosynthesis. The formation of sedoheptulose 7-phosphate takes place according to the following reaction. *Transketolase* requires thiamine pyrophosphate (TPP) and Mg^{++} as co-factors.



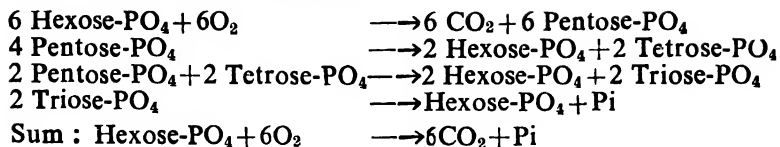
7-carbon sugar, sedoheptulose 7-phosphate is then involved in a reaction with 3-phosphoglyceraldehyde to yield fructose 6-phosphate and a 4-carbon sugar, erythrose 4-phosphate with the help of an enzyme *transaldolase*. Finally to complete the pentose phosphate pathway, the erythrose-4-phosphate can accept the C_2 -unit from xylulose-5-phosphate in a reaction catalyzed by *transketolase* to form fructose 6-phosphate and 3-phosphoglyceraldehyde. The remaining 3-carbon portions of pentose phosphate unite in pairs to yield a molecule of fructose 1, 6-diphosphate by the enzyme *aldolase*. From fructose 1, 6-diphosphate with the removal of one phosphate group with the help of enzyme *phosphatase* gives a molecule of fructose 6-phosphate.

For each complete cycle involving six molecules of hexose, five molecules reappears at the end while there is a net gain of six molecules of carbon dioxide and six molecules of water. The overall change of aerobic respiration should be therefore :



It is evident from the cycle that $NADP^+$ is reduced in the conversion of 6-phosphogluconic acid and ribulose 5-phosphate and since this pathway completes with six turns of the cycle, twelve molecules of reduced $NADP^+$ would be formed. This reduced $NADP^+$ ultimately through an electron transport system will give twelve molecules of water where it will require six molecules of oxygen (refer the topic electron transport system). Since for six turns of the cycle six molecules of water are required in the synthesis of 6-phosphogluconic acid, the net gain of water is six molecules. For each turn of the cycle six molecules of ATP will be formed. So net gain of ATP will be 36 molecules for the complete six turns of the cycle.

Overall summary of reactions :



6 molecules of water would be formed in the process and 36 ATP molecules per molecule of hexose oxidised.

The pentose phosphate pathway therefore clearly provides a means for interrelating the metabolism of hexoses, pentoses, heptoses and tetroses. Since majority of the reactions are reversible, it is possible to produce pentoses from hexose and triose phosphate. This pathway produces a non-oxidative as well as an oxidative route for producing ribose and other pentoses from the hexoses commonly encountered in metabolism. This pathway is intimately involved with the inter-conversion of carbon compounds produced in the initial stages of photosynthesis. The leaves of higher plants do indeed metabolize glucose largely by this pathway. In plants there is also evidence that the prominent pathway in young meristematic tissue is that of glycolysis and that the pentose phosphate pathway achieves more significance as the tissue matures.

15.9 Oxidation-reduction or redox potentials : Some metals like platinum and gold have a very low solution tensions and are essentially inert when placed in solution. They are, therefore, of much value as electrodes¹ for indicating potentials superimposed on them through the oxidation-reduction systems. These types of potentials, in which electrodes take no chemical part, are referred to as an *oxidation-reduction potentials* or *redox potentials*.

The redox potential of an element i.e. its tendency to give up or take on electrons, is a characteristic property of an element and which depends purely on the nuclear and electronic constitution of the element. One of these elements, like hydrogen, give up electrons readily and form ions in solutions whereas others like oxygen take up electrons instead.

Electrode potential is usually measured by immersing the element as an electrode into a solution or one of its salts and then connecting the electrode to a potentiometer. Potential difference is usually measured from the difference between it and the standard electrode, which is also connected to the potentiometer, as a base line. Like hydrogen, zinc also easily forms ions, when they immersed as an

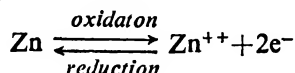
¹ An 'electrode' is a device for conducting electrons to or from an electrolyte solution, an electric arc or a vacuum tube. The electrode is usually made of metals or a metal and one of its salts. Hydrogen, though a gas, may serve as an electrode if the gas is adsorbed on some inert metal like platinum.

TABLE 9

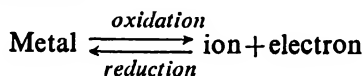
Normal oxidation-reduction potential of some biologically important systems.
Values for pH 7

System	Potential <i>E'</i> 0 (volts) at pH 7.0
α -Ketoglutaric acid \rightleftharpoons Succinic acid + CO_2 + 2H^+ + 2e^-	-0.680
Ferredoxin - Fe^{+++} + $\text{e}^- \rightarrow$ Ferredoxin - Fe^{++}	-0.432
Formate \rightleftharpoons CO_2 + H_2	-0.420
$\text{H}_2 \rightleftharpoons 2\text{H}^+ + 2\text{e}^-$	-0.414
$\text{NADH} + \text{H}^+ \rightleftharpoons \text{NAD}^+ + 2\text{H}^+ + 2\text{e}^-$	-0.317
$\text{NADPH} + \text{H}^+ \rightleftharpoons \text{NADP}^+ + 2\text{H}^+ + 2\text{e}^-$	-0.316
$\text{FADH}_2 \rightleftharpoons \text{FAD} + 2\text{H}^+ + 2\text{e}^-$	-0.219
$\text{FMNH}_2 \rightleftharpoons \text{FMN} + 2\text{H}^+ + 2\text{e}^-$	-0.219
Lactic acid \rightleftharpoons Pyruvic acid + 2H^+ + 2e^-	-0.180
Malic acid \rightleftharpoons Oxaloacetic acid + 2H^+ + 2e^-	-0.102
Reduced flavin enzyme \rightleftharpoons Flavin enzyme + 2H^+ + 2e^-	-0.063
Luciferin \rightleftharpoons Oxyluciferin + 2H^+ + 2e^-	-0.050
Ferrocyclochrome <i>b</i> \rightleftharpoons Ferricyclochrome <i>b</i> + e^-	-0.040
Succinic acid \rightleftharpoons Fumaric acid + 2H^+ + 2e^-	-0.015
Decarboxylase	+0.190
Ferrocyclochrome <i>c</i> \rightleftharpoons Ferricyclochrome <i>c</i> + e^-	+0.260
Ferrocyclochrome <i>a</i> \rightleftharpoons Ferricyclochrome <i>a</i> + e^-	+0.290
Ferrocyclochrome <i>a</i> ₃ \rightleftharpoons Ferricyclochrome <i>a</i> ₃ + e^-	?
$\text{H}_2\text{O} \rightleftharpoons \frac{1}{2}\text{O}_2 + 2\text{H}^+ + 2\text{e}^-$	+0.815

electrode in a solution of one of its salts. Thus in zinc, the release of electrons takes place



Or in other words :



The hydrogen electrode is used to determine the potential of another electrode. The potential of 'normal' hydrogen electrode is arbitrarily taken as 0.0. The electrode whose potential is to be determined is placed on other side. The potential difference between these two electrodes is measured by a potentiometer.

An atom, therefore, by the release of electrons becomes a positively charged ion and acts as a reducing agent (reductant). The greater its tendency to release electrons, the greater is its reducing potential. Conversely, anything which accepts an electron, like oxygen or copper ion, is an oxidising agent (oxidant). The greater

its tendency to accept electrons, the more is its oxidising potential. Electrode potential, therefore, is a measure of the oxidation and reduction capacity of the element.

The study of these oxidation-reduction potential or redox potential in biological system is of immense importance as it determines the particular sequence of reactions occurring in a cell. In the biological system most pertinent questions that lie before us, why the dehydrogenase enzymes remove electrons from the substrate and pass it to flavoproteins? And why do these flavoproteins pass the electrons to cytochromes which ultimately transferred these to oxygen? With the help of oxidation-reduction potential it is now possible to give a reasonable explanation of all the above critical sequences. From the table 9 it is evident that each enzyme system develops a characteristic redox potential and this range lies between hydrogen electrode at one end and oxygen electrode at the other. It is further evident that these enzyme systems and substrates in a cell can reduce the one below it and oxidise the one above it.

In biological redox system fifteen such metabolic functions have been studied. These values, however, do not correlate with the theoretical values, because the derivation of redox equation depends on a system in equilibrium and in living system, such an equilibrium is never reached.

15.10 Significance of Krebs cycle :

(i) A large amount of energy is produced in this cycle. Each turn of the cycle produces 15 molecules of ATP. Major part of energy liberated during respiration is obtained in this cycle.

For every turn of oxidation-reduction of coenzymes 3 ATP molecules would be formed. So, the net gain for complete cycle is 36 molecules of ATP.

The energy is then utilized by plants in the absorption of electrolytes, translocation of solutes, growth, movements etc.

(ii) This cycle opens up the possibility of pyruvic acid being diverted to other metabolic pathways.

(iii) In addition to its oxidation of the substrate and the generation of ATP molecules, this cycle is also responsible for the production of large number of plant acids.

(iv) This cycle is intimately connected with nitrogen metabolism particularly with the synthesis of amino acids (refer article 10.5). The organic acids which are formed in this cycle form a key substrate in the synthesis of amino acid.

(v) The formation of key intermediates in the breakdown of carbohydrate is very significant in the synthesis of many compounds of biological interest.

(vi) According to Krebs, the mechanism by which interconversion of organic acid results represent a general scheme for carbohydrate metabolism.

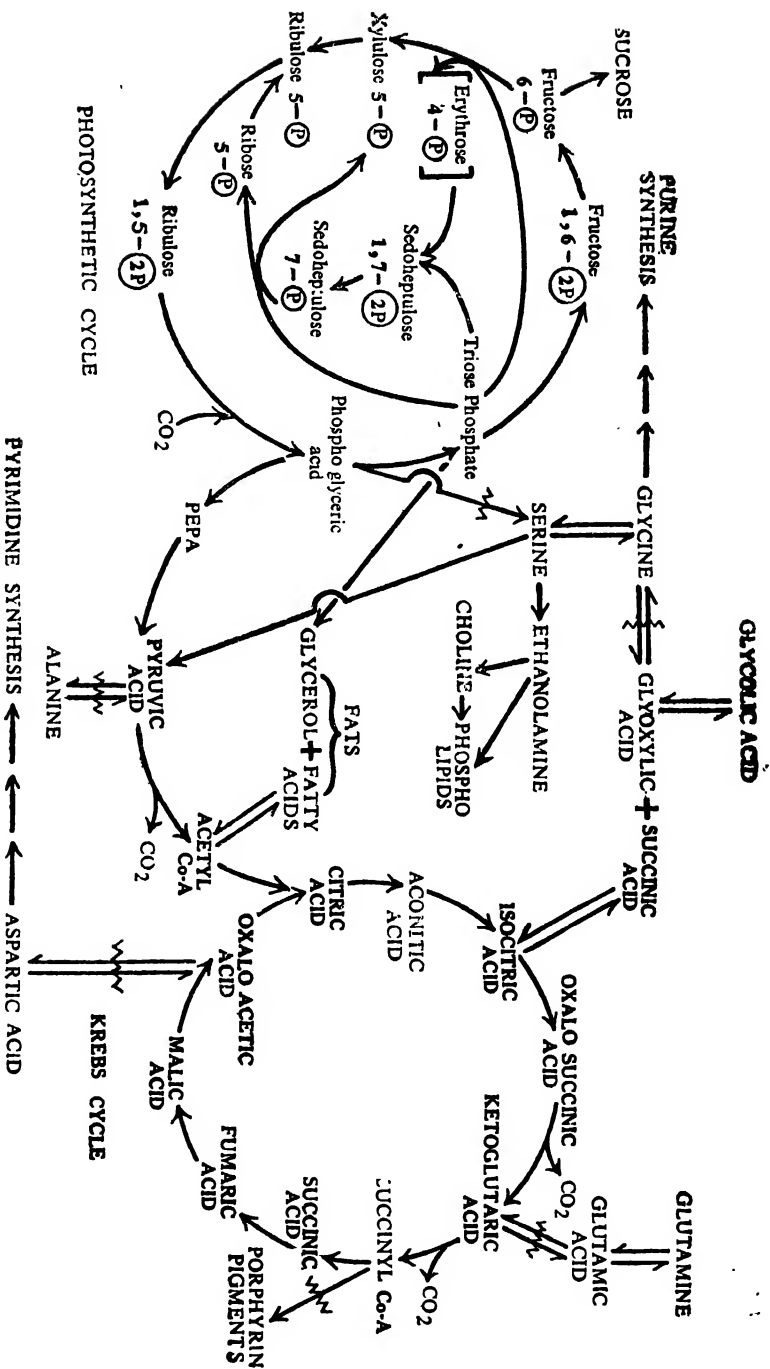


Fig. 5.15.9 Interrelations between photosynthesis, respiration and other bic-synthesis in the green plant cell. (modified after Giese, 1968).

The interrelationship of organic acids with the different metabolism of plants is shown in Fig. 15.9.

15.12 Relation between aerobic and anaerobic respiration : That a close connection exists between these two processes was first demonstrated by Pflüger (1875) in certain animals. He suggested that the respiratory material was first broken up anaerobically into carbon dioxide and easily oxidisable products, the latter is then oxidised by atmospheric oxygen to carbon dioxide and water.

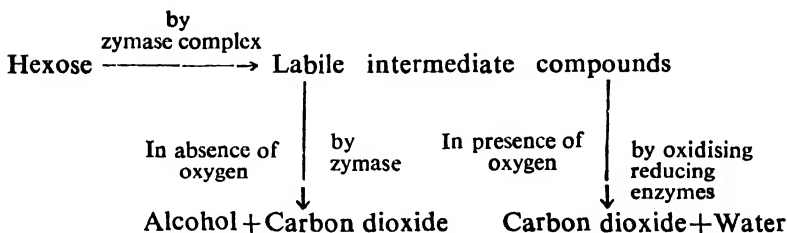
Pfeffer (1878) took up the above view and suggested that respiration took place in two stages :

(i) the splitting of sugar by a number of steps into alcohol and carbon dioxide ; and

(ii) alcohol or some other products formed in one of the steps of the former process is oxidised to carbon dioxide and water.

The first of these stages is independent of oxygen and is called anaerobic respiration.

The above idea has been modified by Kostytschew and according to him the relation between the two processes may be represented as :



According to him sugar is first converted to a labile intermediate product by the enzyme, zymase complex in both types of respiration. After this the course of respiration depends upon the availability of oxygen. If oxygen is not available, the reaction starts anaerobically by zymase complex producing alcohol and carbon dioxide. If on the other hand oxygen is available, the intermediate products undergo oxidation by the influence of oxidising reducing enzymes producing carbon dioxide and water.

The following are the evidences which suggest the connection between aerobic and anaerobic respiration :

(i) Anaerobic respiration of aerobic plant when deprived of oxygen appears to be an universal phenomenon with the only exception of *Elodea cann. densis*.

(ii) The enzyme, zymase complex, concerned with the anaerobic splitting of sugar appear to be universally present in all plant cells. Here it reacts with the carbohydrate, producing intermediate products just like anaerobic process and the latter, however, is utilized in the oxidation process of aerobic respiration.

(iii) A period of anaerobic respiration should lead to the accumulation of easily oxidisable substance. So if a plant is transferred from anaerobic to aerobic condition a rapid and temporary increase in the rate of respiration takes place due to rapid oxidation of oxidable substance.

(iv) It has been mentioned that acetaldehyde which is in all probability an intermediate product of anaerobic respiration, has also been demonstrated in the normal aerobic respiration (Klein Prisett).

Differences between aerobic and anaerobic respiration

Anaerobic

1. The whole process of anaerobic respiration goes in complete absence of oxygen.
2. The ultimate products of anaerobic respiration are ethyl alcohol and carbon dioxide.
3. The process of oxidation is relatively small and so energy liberated is small (about 27 Kgcal).
4. The oxidation-reduction process takes place within the products of the original molecule.
5. The degradation of pyruvic acid is effected by a simple reaction.
6. A fraction of the intermediate products of glycolysis never built back to the system i.e., oxidative anabolism (OA) does not occur.

Aerobic

1. A portion of the process can go in absence of oxygen while for the rest of the process oxygen is essential for its completion.
2. The ultimate products are always carbon dioxide and water.
3. The oxidation in this process is far greater and so energy liberated is also great (about 673 Kgcal).
4. The oxidation of the carbohydrate takes place with molecular oxygen which serves as the ultimate electron acceptor.
5. Pyruvic acid is always oxidatively consumed in a complex cycle known as Krebs cycle.
6. A fraction of the intermediate products of glycolysis is always built back. This type of anabolic resynthesis (i.e. oxidative anabolism) always takes place in aerobic respiration.

Relation between fermentation and anaerobic respiration : Fermentation and anaerobic respiration are basically similar if not identical processes. There are several facts in favour of this view.

(i) In fermentation hexose sugar is utilized and the same is frequently the case in anaerobic respiration. When some substances other than hexose sugar is utilized it is only possible if the substance is transformed to hexose sugar before being utilized in respiration.

(ii) In both the processes carbon dioxide is produced, while in fermentation like anaerobic respiration, the formation of ethyl alcohol too has been demonstrated.

Thus as far as it is known both substrate and end products in anaerobic respiration are same as in alcoholic fermentation.

(iii) All the enzymes which play their respective roles in various stages of fermentation have also been isolated from higher plants suggesting that metabolism for both the process is same.

(iv) Neuberg has shown that acetaldehyde is formed as an intermediate product of fermentation and the blocking of the reaction will proceed if sulphite was added and acetaldehyde could be found to accumulate. Similar blocking of anaerobic respiration in pea has also been demonstrated by Neuberg and Cohen.

(v) The process of fermentation is accelerated by the addition of soluble phosphate, while the addition of phosphate in the tissues of higher plants also leads to an increased rate of carbon dioxide and alcohol production. The reasons behind this are very variable and contradictory.

Even if we have the question of effect of phosphate doubtful the evidences already cited in favour of the view that alcoholic fermentation is the same process as anaerobic respiration is very strong.

Dissimilarity between fermentation and anaerobic respiration :

(i) Anaerobic respiration generally takes place in higher plants while alcoholic fermentation occurs in yeasts and other microorganisms.

(ii) In fermentation certain substances may be formed in addition to or instead of ethyl alcohol as end products ; while in anaerobic respiration ethyl alcohol is always formed.

(iii) Anaerobic respiration is generally intracellular while alcoholic fermentation is extracellular.

(iv) In anaerobic respiration the end products are oxidatively consumed in subsequent aerobic process. In fermentation, however, the end products are either accumulated or escape from the cell.

(v) Fermentation takes place with zymase complex whereas anaerobic respiration takes place with a number of specific enzymes.

15.13 Enzymes in respiration : A large number of enzymes is involved in the process of respiration. Majority of them are responsible for the oxidation-reduction system in plants. A number of co-enzymes are also taking part in this oxidation-reduction system.

The idea regarding the enzymes involved in respiration followed after the discovery of *zymase* in 1903 when it was considered to be a single enzyme. After that it has been found that the enzymes present in the zymase complex are also found in higher plants.

The pioneer workers in the line of enzyme study are Tanko (1936). James (1940-41) and Hanes (1940). The whole reaction sequence upto glycolytic stage can be divided into (i) formation and phosphorylation of starch, (ii) interconversion of hexose phosphate and (iii) transformation of 3-carbon sugars.

I. Formation and phosphorylation of starch :

(a) *Q-enzyme*—Q-enzyme converts linear amylose¹ directly to amylopectin¹ in the absence of inorganic phosphate and phosphorylase.

This enzyme has been named by Peat (1945) and differs from the *phosphorylase*—called the P-enzyme which can catalyze the formation of amylose from glucose 1-phosphate.

(b) *Phosphorylase*—This enzyme has been discovered by Hanes (1940) and great attention has been paid to its nature and role in plant tissues. It converts starch to glucose 1-phosphate.

II. *Interconversion of hexose phosphate*—It includes the stages of breakdown from glucose 1-phosphate to fructose 1-6 diphosphate.

Evidences available concerning the enzymes involved in the conversion of glucose 1-phosphate to fructose 1-6 diphosphate came from the work of Tanko (1936) and Hanes (1940). *Hexokinase*, *phosphohexo isomerase* and *phosphofructokinase* are the examples of enzymes involved in this conversion (For detail refer article 15.5).

III. *Transformation of 3-carbon sugar*—It includes the stages of reactions involved in the conversion of 3-phosphoglyceraldehyde (3-PGAld) to pyruvic acid (PA) (For detail refer article 15.6).

The enzymes in the breakdown of PGAld to PA have been studied by James (1949), Stumpf (1950) and others.

Aldolase, *isomerase*, *triose-phosphate dehydrogenase*, *transphosphorylase*, *phosphoglyceromutase* and *enolase* are the examples of enzymes involved during 3-carbon sugar conversion.

IV. *Enzymes of the Krebs cycle*—Enzymes which are responsible for the breakdown of pyruvic acid in presence of oxygen are mainly of *dehydrogenase* and *decarboxylase* types. Of the dehydrogenase the most important are *isocitric dehydrogenase*, *succinic dehydrogenase* and *malic dehydrogenase* which convert isocitric acid to oxalosuccinic acid, succinic acid to fumaric acid and malic acid to oxaloacetic acid respectively. The most important decarboxylase are *oxalosuccinic decarboxylase* and α -ketoglutaric *decarboxylase*. These convert oxalosuccinic to α -ketoglutaric and further to succinic acid.

Together with enzymes are some of the co-enzymes with includes Co-A, NAD⁺, NADP⁺, flavin as well as cytochromes.

15.14 Photosynthesis/Respiratory (P/R) ratio : In the case of maize, the rate of photosynthesis during the daytime hour is, on an average, about eight times the rate of respiration (Transean, 1926). Almost similar conclusion have been obtained by Thomas and Hill (1937) on alfalfa. It means that in the leaves and other green tissues the rate of photosynthesis is always exceeds the rate of respiration during the day time. The carbon dioxide released in respiration is

¹ Amylose and amylopectin are the two components of starch.

TABLE 10
Enzymes involved in the Krebs cycle

Reaction	Enzyme	Inhibitor
Pyruvic acid and acetyl Co-A	Oxidative decarboxylation system	—
Acetyl Co-A and oxaloacetic acid	Condensing enzyme	—
Citric acid to <i>cis</i> -aconitic acid	Aconitase	Fluorocitrate
<i>Cis</i> -aconitic to isocitric acid	Aconitase	—
Isocitric to oxalosuccinic acid	Isocitric dehydrogenase ; NADP ⁺	Anaerobiosis
Oxalosuccinic to α -ketoglutaric acid	Oxalosuccinic decarboxylase Mn ⁺⁺	—
α -Ketoglutaric to succinic acid	Oxidative decarboxylation	Arsenite
Succinic to fumaric acid	Succinic dehydrogenase	Malonate
Fumaric to malic acid	Fumarase	—
Malic to oxaloacetic acid	Malic dehydrogenase ; NAD ⁺	—

fully utilized in photosynthesis, but since photosynthesis occurs more vigorously than respiration, additional carbon dioxide must diffuse into the plant from the environment. Similarly, photosynthesis produces more oxygen than is used in respiration and so the excess oxygen diffuses out of the plant. Hence during the daytime hours, there is a net movement of carbon dioxide and oxygen between the leaf and the environment.

At night the reverse condition prevails i.e. oxygen moves into the green parts and carbon dioxide is given off from the plant. For the non-green parts of the plant this is the usual exchange procedure in the light or in the dark.

Since at low light intensities the rate of photosynthesis decreases, a point will therefore reach when the rate of photosynthesis in a leaf or green parts of the plant is exactly equal to the rate of respiration. At this light intensity, often called a *compensation point*, volume of carbon dioxide released in respiration is exactly equal to the volume being utilized during photosynthesis, the opposite is true for oxygen. So at this point there is no gaseous exchange. *A compensation point can therefore be defined as a point in light intensity when no gaseous exchange is observable between the photosynthetic organ and the environment illuminated by that light intensity.* The light intensity corresponding to the compensation point varies considerably in different species of plants. Thus the compensation point for shade plants is about 50-100 ft. candles while its value is 100-200 ft. candles for sun plants.

At compensation point there is no net gain in organic matter. On the contrary, there will be a loss of organic matter due to respiration by non-green parts and dark respiration. So, continued illumination at this point will therefore, kill the plant. Hence the

actual minimum light intensity at which any plant could survive would necessarily be somewhat greater than the compensation point.

At the compensation point, the rate of photosynthesis is exactly equal to the rate of respiration and so the ratio between them i.e. P/R ratio is unity. So at this point the sugar synthesized in photosynthesis is completely utilized in respiration. Further, if the P/R ratio is less than one, it is evident that respiratory breakdown is in excess of photosynthetic manufacture of food. In both these cases plant not survive. Healthy growth of the plant is only possible when the P/R ratio is greater than one. Because under this condition more sugar is left by the plant for night respiration. Greater the P/R ratio the more possibility of accumulating organic matters by the plants.

Moderately, high day-time temperature and comparatively cool night temperature is favourable for the greater P/R ratio and thus favouring greater accumulation of organic matters. So, the storage plant like potato is favourably grow under such condition. Actually, under ordinary favourable growing conditions plants usually have a P/R ratio of around 5 or even more. Thus there is an abundance of food that can be used in respiration and assimilation, with a surplus that accumulates.

15.15 Factors affecting the rate of respiration: All the foregoing discussions clearly indicate the complex nature of the process which consists of a series of biochemical changes and is intimately linked with the living processes. So, like all biochemical processes, the rate of respiration is also controlled by a number of internal and external factors. The respiratory process is normally evaluated by the gas exchange mechanism and which does not constitute an absolute indicator of respiratory intensity but is usually defined as apparent respiration rate. The principal external factors which can affect the rate of respiration considerably, include oxygen, temperature, carbon dioxide concentration, light, injury, water supply, effect of chemical compounds, inorganic compounds. Of internal factors protoplasmic condition of the cell, water content of the cell, respiratory substrate are important.

External Factors :

(i) *Oxygen concentration of the air*—The concentration of oxygen of the air is one of the most important factors which affect the rate of respiration considerably. Generally the respiratory rate increases with increase in the oxygen concentration of the atmosphere. If the oxygen concentration falls below 50%, the rate of respiration decreases, while the rate increases with increase in the concentration of oxygen. Thus the rate of respiration is directly proportional to the oxygen concentration in plants.

(ii) *Temperature*—Generally an increase in temperature upto certain limit increases the rate of respiration. An increase in the respiration rate generally takes place within a temperature range

between 0° and 45°C ; above 45°C the rate falls and finally the process stops. It has been found that the rate of respiration decreases with time (time factor) at a temperature above 30°C ; this decrease is possibly due to the destruction of protoplasm and enzymes. It was noticed that within the temperature range (0°C — 35°C) respiration rate to temperature effect follows Vant's Hoff's law, where for every 10°C rise in temperature, the rate of reaction becomes doubled i.e. Vant's Hoff's coefficient is generally two ($Q_{10}=2$).

(iii) *Carbon dioxide concentration*—There is a direct inhibitory effect of carbon dioxide concentration on the respiration rate. Carbon dioxide concentration however does not always have inhibitory effect on the rate, as the high concentration of carbon dioxide in the leaves may have a higher rate of respiration. High concentration of carbon dioxide incidentally, results in the accumulation of more sugar, a substrate for respiration, consequently increases the rate of respiration.

(iv) *Light*—Light has mainly an indirect effect on the rate of respiration. In case of non-green plants the rate of respiration is increased when exposed to light. Again in some cases enhancing effect of light on the respiration rate is also noted (Emerson and Lewis, 1940). A direct effect of light on the respiratory rate has been demonstrated by Weintraub and Johnston (1944). In green plants, light plays an important role in the rate of respiration, by the formation of respiratory substrates as a result of photosynthesis.

(v) *Injury*—Generally in case of injured plant tissues the rate of respiration is increased for the time being. This increase gradually rises to a maximum point after which a decrease in the rate results. This increased rate of respiration may be due to high accumulation of sugar to about 70% around the injured cells (Hopkins, 1927).

(vi) *Chemical compounds*—Chemical substances like chloroform, acetone, ether etc. bring about a temporary increase in the rate of respiration. Their activity is not pronounced at a lower concentration; a higher concentration, being toxic, decreases the rate of respiration.

(vii) *Inorganic salts*—Chlorides of different metals like sodium, potassium, magnesium, calcium have a pronounced effect on the rate of respiration. Monovalent chlorides (e.g. NaCl , KCl etc.) increase while the divalents (e.g. CaCl_2 , MgCl_2 etc.) decrease the rate of respiration.

Internal Factors :

(i) *Protoplasmic condition*—The respiratory rate is always higher in young cells which are rich in protoplasm than the older cells having scanty protoplasm. Besides this, some other internal conditions of protoplasm also influence the rate of respiration. Hydration of the protoplasm and the quantity of the respiratory enzymes in the mitochondria are the important protoplasmic factors. The rate of

respiration is higher in young cells and in the actively growing cells than the old mature cells, due to large amount of active protoplasm in the former.

(ii) *Water content of the cell*—It greatly influences the respiratory rate as the water present in the cell increases the amount of soluble respiratory substrate and also the activity of the protoplasm by the enzymes.

(iii) *Respiratory substrate*—The rate of respiration is directly proportional to the respiratory substrate present in the tissues. High concentration, however, has an adverse effect. In high concentration of sugar, rate of respiration decreases due to high osmotic value.

15.16 Experiments on respiration :

(i) *Experiment to show the evolution of carbon dioxide during aerobic respiration*—Few germinating seeds are kept in a round bottomed flask fitted with a holed cork at the mouth. Pieces of caustic potash sticks are introduced into the neck of the flask. At the base of the neck cotton plug is also inserted. Now a long glass tube is introduced through the hole of cork and the whole system is then inverted over a trough of mercury and kept in a position with the help of a clamp (Fig. 15.10). Precaution should be taken that the free end of the tube does not touch the bottom of the mercury trough and the fitting must be air tight to avoid any leakage. After few hours it will be found that mercury has risen in the tube. This can be explained on the basis that carbon dioxide thus produced by the germinating seeds has been absorbed by KOH sticks, hence a vacuum was created as a result mercury in the tube has risen.

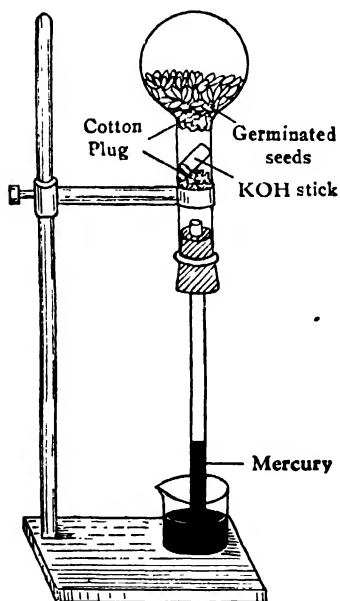


Fig. 15.10 Experiment demonstrating aerobic respiration in plant material.

can be proved by introducing a bit of caustic potash (KOH) stick into the test tube when the gas is absorbed and the mercury column again rises filling up the tube.

(iii) *Experiment to show the heat release during respiration*—A thermos bottle (Dewar's flask Fig. 15.12) was taken and was fitted with a cork through which passes a thermometer. Another set was prepared likewise some dry seeds in one and some moist seeds (germinated seeds) were introduced in the other. The flasks were sealed properly and left for few hours. After that period examine

(ii) *Experiment to show the evolution of carbon dioxide during anaerobic respiration*—Fill a test tube with mercury and inverted over a mercury basin vertically with the help of a clamp on a stand. Some pea seeds (soaked in boiled but cooled water) are taken and then seed coats are peeled off; they are now introduced by the help of a bent forceps in the test tube and will collect at the top of the test tube (Fig. 15.11A). Observation from time to time reveals that a gas forms at the top of the test tube by the displacement of mercury in the test tube (Fig. 15.11B). The gas is CO_2 .

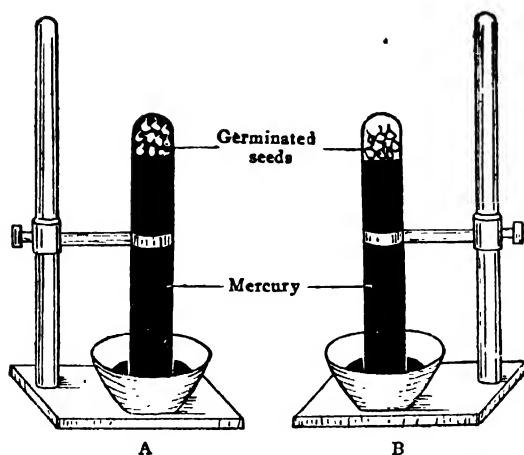


Fig. 15.11 Experiment demonstrating anaerobic respiration of seeds.

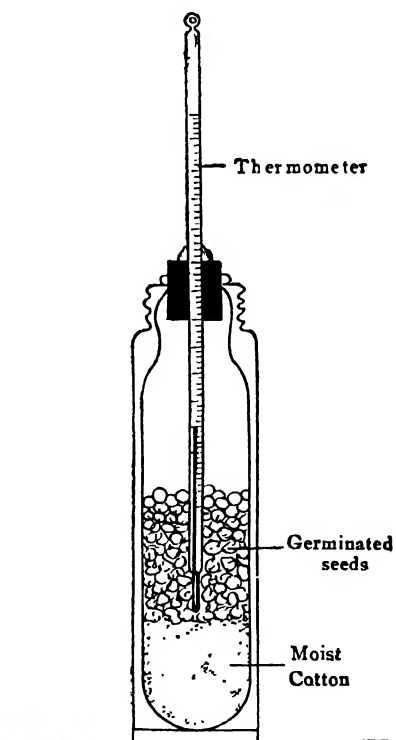


Fig. 15.12 Experiment demonstrating release of heat during respiration.

the rise of temperature in the flask containing moist seeds. The temperature, however, remains unchanged in the flask containing dry seeds. This clearly suggests that during respiration considerable amount of energy (in the form of heat) released which causes an increase in the temperature.

(iv) *Quantitative estimation of carbon dioxide evolved during respiration*—The basic principle of this experiment is to allow the tissues to respire in a carbon dioxide free air and to measure the amount of carbon dioxide evolved after respiration. Five same sized conical flasks were taken and the whole set was set up according to the diagram (Fig. 15.13). The first flask (A) contains normal (N)

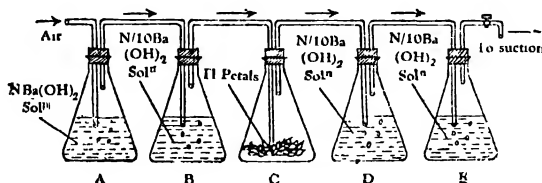


Fig. 15.13 Experiment for quantitative estimation of carbon dioxide during respiration.

$\text{Ba}(\text{OH})_2$ solution to absorb carbon dioxide of the atmosphere coming through the tube, the second flask (B) containing $\text{N}/10 \text{ Ba}(\text{OH})_2$ solution serve as a check to absorb all carbon dioxide if it escapes from the previous flask, so that the air passes to the third flask (C) is completely free of carbon dioxide. The flask (C) contains measured amount of flower petals. Last two flasks (D and E) contains known amount (50 ml) of $\text{N}/10 \text{ Ba}(\text{OH})_2$ solution. This solution may be coloured with phenolphthalein—to indicate its alkalinity. If during experiment the solutions become colourless, stop the flow of air and add a fresh 20 ml of $\text{N}/10 \text{ Ba}(\text{OH})_2$ solution. Flask E contains $\text{N}/10 \text{ Ba}(\text{OH})_2$ solution for the final check to absorb all carbon dioxide, liberated during respiration.

After placing the flower petals in the respiration chamber (flask C) quickly check all connections to make sure that the flasks are all air tight and start the suction pump.

Allow the apparatus to operate for 12 hours during which period the carbon dioxide liberated by the flower petals due to respiration will be precipitated as BaCO_3 in the flask (D) and also in E to some extent.

Pipette out exactly 5 ml of the content from D to a test tube and a drop of phenolphthalein and then titrate the residual $\text{Ba}(\text{OH})_2$ in the solution with standardized $\text{N}/10 \text{ HCl}$.

A blank titration was made containing $\text{N}/10 \text{ Ba}(\text{OH})_2$ in exactly the same way and then calculate the amount of carbon dioxide evolved by flower petals from the following equation.

$$\text{CO}_2 \text{ in milligrams} = V \times N \times 22.0$$

where V = difference between the blank and experimental titration in ml

N = normality of HCl used in titration.

and 22.0 = normal wt. of CO_2 .

From the experimental data calculate the mg of carbon dioxide evolved per hour per g of fresh weight of the plant material.

(v) *Experiments on RQ* :

(a) *By a pair of respiroscope*—The RQ can be determined by a simple apparatus fixed on a wooden frame (Fig. 15.14) which consists of two vertical tubes. Both the tubes contain same amount of germinated seeds (with seed coat removed) and the narrow end of the tube dip into a beaker containing saline water. Upper end of the tubes is closed by means of corks through which pass two small glass

tubes ended with a stop cock. From the upper end of the tube B hang a small tube which contains some KOH pellets.

The stop cock is then connected by means of a rubber tubing and by opening the stop cock the air is sucked out till the water rises through the lower narrow tube upto certain height. Close the stop cock and mark the level of the water in the tube in both the cases.

After few hours note the change in the level of the water column in the tubes and from that reading the RQ can be determined. The unchanged position of water level in A after experimental period indicates the volume of carbon dioxide produced is equal to the volume of oxygen absorbed. The rise in the level is, however, due to consumption of more oxygen than carbon dioxide liberation. Whereas fall in the level indicates that it is due to more carbon dioxide liberation.

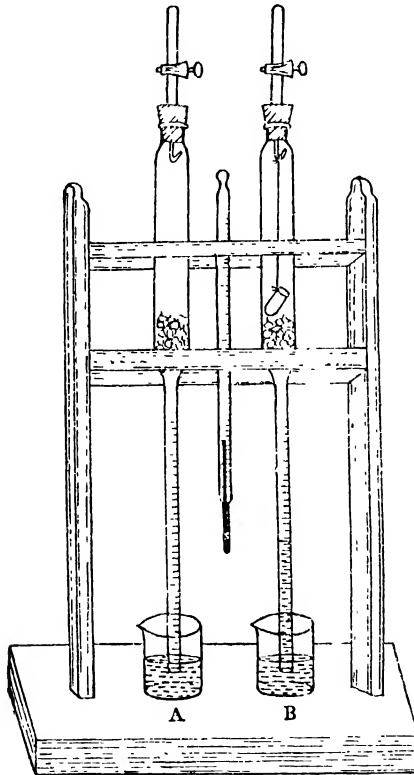


Fig. 15.14 A pair of respiroscope.

and less oxygen absorption. The rise of water level in B is due to absorption of carbon dioxide by KOH and will indicate the amount of carbon dioxide liberated by the plant material during respiration. This amount is also equivalent to the amount of oxygen absorbed when the plant material is a carbohydrate storing seeds and the RQ is consequently one. In case of fatty seeds the rise in the level in A indicates that more oxygen is absorbed than carbon dioxide evolution and the RQ is less than one. So by simply noting down the change of the level of water in the vertical tubes of the apparatus the RQ of the material can be demonstrated.

Thus if no change in the level of water takes place in A the RQ is one. The rise in the level in A indicates that RQ is less than one and a fall in the level of water in A indicates that RQ is more than one.

(ii) *By Ganong's respirometer*—The apparatus consists of three parts—(i) a bulb provided with a stopper at its tip and may be opened or closed by turning the stopper (ii) a graduated manometer tube and (iii) a levelling tube connected with the manometer tube by means of a rubber tubing (Fig. 15.15). The volume of the bulb and the graduated manometer tube is exactly 102 ml 2 ml of germinated pea seeds were placed in the bulb so that the volume in the manometer tube is exactly 100 ml

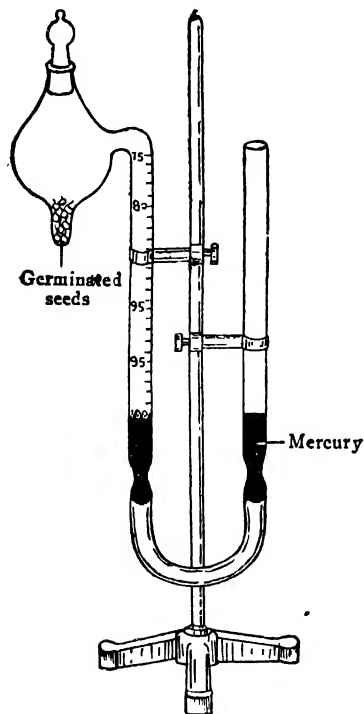


Fig. 15.15 Ganong's respirometer.

of oxygen absorbed is equal to the volume of carbon dioxide liberated and the volume of carbon dioxide liberated can be determined by adding KOH pellets to the solution.

If fatty seeds like castor, mustard etc. are used instead of pea seeds and saturated sodium chloride is added to the tube, there is a rise in the level of salt solution after the experimental period. This rise is due to the greater absorption of oxygen. If now KOH pellets were introduced then there is again a rise of the solution. This latter rise indicates the amount of carbon dioxide liberated during respiration. Whereas the sum total of both these rises indicate the volume of oxygen utilized by the respiring materials. Thus RQ is less than one.

(v) *Experiment to demonstrate the continuity of intercellular spaces*—A conical flask is filled up about $\frac{3}{4}$ th with water and is fitted with a double bored cork, through one of which insert a long petioled leaf of *Colocasia* so that the petiole remains within the water. Through another hole insert a bent glass tube as in Fig. 15.16 and connect with a suction pump. Make all connections airtight and draw out air from the bottle by suction pump and bubbles would appear to come out of the petiole into the water of the bottle.

Pour 10% KOH solution from the side tube and now rotate the stopper of the bulb until an air connection is made. Now by adjusting the side tube keep the solution level at 100 ml. So that the respiratory materials are in contact with 100 ml. of air.

Now, close the stopper and cut all air connections from the tube with the surrounding air. Carbon dioxide produced in respiration will be absorbed by KOH solution and consequently there is a rise of the level of KOH in the manometer tube. Suppose there is a rise of liquid (KOH) upto 80 ml. It indicates that the 20 ml of carbon dioxide have been evolved and have been absorbed by KOH. So there is a rise upto 80 ml.

Since $\frac{1}{3}$ th of air is oxygen and that amount (20%) is found to be utilized by the plant material for respiration. So the rate of movement of KOH solution can be taken as the rate of oxygen absorption by the respiratory material and consequently RQ is exactly one.

This experiment can also be set by adding mercury or saturated saline solution to the manometer tube instead of KOH solution. In the latter two cases there will be no appreciable rise in the level of solution in the tube indicating the volume

of oxygen absorbed is equal to the volume of carbon dioxide liberated and the volume of carbon dioxide liberated can be determined by adding KOH pellets to the solution.

It shows that as the air is sucked the atmospheric air enters through the stomata of the leaf and through the intercellular spaces ultimately comes out through the petiole.

Similar experiment can also be set up by inserting a woody twig, the cut ends of which are closed. The atmospheric air in this case passes through the lenticel (as both the cut ends are closed) to the intercellular spaces and again bubble will come out in water through the lenticel of the submerged portion of the twig.

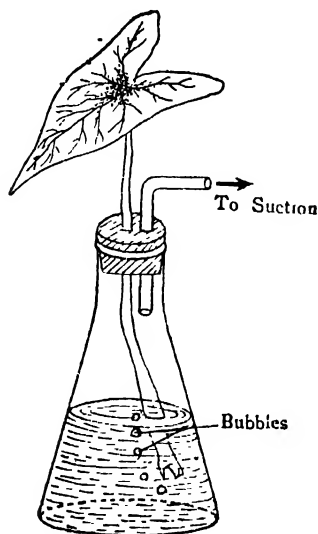


Fig. 15.16 Arrangements demonstrating continuity of intercellular spaces in a leaf.

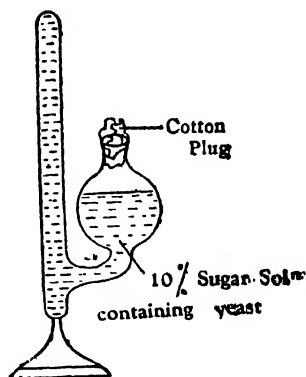


Fig. 15.17 Kuhne's fermentation vessel.

(vii) *Alcoholic fermentation*—Prepare about 50 ml of approximately 2% solution of glucose. Dissolve some baker's yeasts in a beaker with small quantity of water and prepare a creamy mixture. Stir this mixture with glucose solution. Now carefully fill the straight arm and half of the bowl of the Kuhne's vessel with this solution (Fig. 15.17). Plug the open end of the vessel with cotton and keep the tube at a temperature of about 30°C. Fermentation soon begins and the carbon dioxide gas begins to collect at the top of the tube. That this gas is carbon dioxide can be proved by introducing a piece of KOH stick which will absorb carbon dioxide and the gradual shrinkage in the volume of the gas takes place.

After a considerable period of fermentation a smell of alcohol may be easily detected by removing the cotton plug.

15.17 Organic acid metabolism :

(i) *Nature and distribution of plant acids*—The compounds which contain a carboxyl ($-\text{COOH}$) group or groups fall into the category of organic acids. Of all types of aromatic and aliphatic organic acids present in higher plants, a group of aliphatic acids—generally known as plant acids—is distinguished by their wide distribution and physiological functions. Many of the important organic plant acids like oxaloacetic acid, α -ketoglutaric acid, malic acid, fumaric acid, glutaric acid etc. are *dicarboxylic* ; whereas citric acid, isocitric

acid, aconitic acid, oxalosuccinic acid are the examples of *tricarboxylic acid*. Some of the acids, however, contain ketone ($-\text{C}=\text{O}$) group and are also known as *keto acids* e.g. oxaloacetic acid, α -ketoglutaric acid, pyruvic acid etc. Many, however, contain hydroxyl ($-\text{OH}$) group in addition to carboxyl group and are known as *hydroxy acids* e.g. malic and, tartaric acid, citric acid, isocitric acid etc.

All plant saps contain a mixture of these organic acids, although their amount varies considerably. Amongst them citric acid is of universal occurrence although it is present in higher concentration in the fruit of citrus. Isocitric acid is an isomer of citric acid and is present in black berry (*Rubus fruticosus*) and in the leaves of succulent plants (e.g. *Bryophyllum*).

Among the 4-carbon dicarboxylic acids, malic acid occurs everywhere in plant tissues and predominates in apples (*Malus sylvestris*), tartaric acid in tamarind (*Tamarindus indica*), malic acid in banana (*Musa paradisiaca*). Succinic and fumaric acids however occur in lower concentration.

Of the keto acids, α -ketoglutaric and oxaloacetic acid have not been the subject of wide inquiry, but have been reported from pea seedlings.

The simplest of all plant acids, oxalic acid is found to be widely distributed and is present in the leaves and fruits of many plants.

(ii) *Metabolism of acids*—Although the presence of organic acids in plants has been known for many years, but the role of these acids remained entirely obscure until recently. Kostytshev (1927) first experimentally showed that these acids are the end products of amino acid metabolism. It was also later on supported by Ruhland. But it is now clear that these plant acids play an important role in cellular respiration. The various interrelation among different groups of organic acids based mainly on the work of Krebs and Johnson—known as Krebs cycle—the details of which have been studied in respiration [refer article 15.6 (ii)]. With the exception of tartaric and oxalic acids, Krebs cycle contains almost all acids present in plants or it may be that through the reactions of Krebs cycle, several plant acids are formed and interconverted.

Accumulation of organic acids in plant is of usual occurrence and is found to be due to block or partial block of a particular step in this cycle. Thus the accumulation of citric acid occurs when *citric dehydrogenase* is not so active in converting citric acid to α -keto glutaric acid.

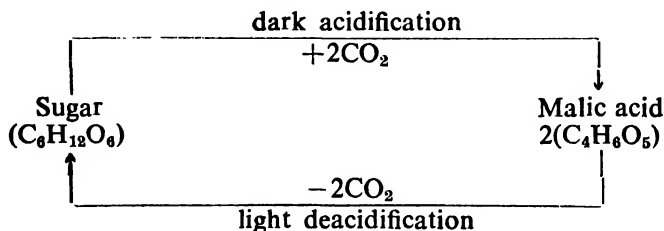
Oxalic acid which does not enter into the Krebs cycle may arise through glyoxylic acid according to

Glycolic acid \longrightarrow Glyoxylic acid \longrightarrow Oxalic acid

Many of the organic acids are related to the synthesis of fatty acids and amino acids. The synthesis of fatty acids and the ultimate synthesis of fats takes place according to the following scheme.

This reaction is known as Wood and Werkman's reaction and is found to be occurring in large number of plants and the organic acids synthesized by the process are utilized in the normal metabolic reactions of the plant. The interrelationship of organic acids with different metabolism of plants is given in Fig. 15.18.

It has been observed that an increase in the titrable acidity during the night or when placed in the dark in the shoots or leaves of some plants under Crassulaceae, Cactaceae etc., occurs where succulence is a common characteristic of the plants. This is known as *dark acidification*. With the return of daylight this amount of titrable acidity decreases significantly. This is known as *light deacidification*. This titrable acidity reaches a minimum value in the late afternoon or early evening. This type of fluctuation of titrable acidity is known as *crassulacean acid metabolism*.



The above scheme is mainly for the accumulation of malic acid. In the dark acidification there is a net consumption of respiratory carbon dioxide with the resulting RQ less than unity but when light deacidification takes place there is a net liberation of carbon dioxide and this causes the RQ to rise above unity.

SELECTED QUESTIONS

1. What is respiration? How does it differ from photosynthesis? Describe an experiment to demonstrate it in a green plant.

Refer article 15.1. For the difference with photosynthesis refer chapter 9. For the last part of the question refer article 15.16(i). In this experiment instead of germinating seeds, some green leaves should be inserted in the round bottomed flask. The whole round part of the flask should be covered with black paper in order to prevent the process of photosynthesis otherwise all carbon dioxide released in respiration could be utilised in photosynthesis.

2. Define RQ. How does it help in determining the nature of the respiratory substrate?

Refer article 15.3. For last part refer the topic *significance of RQ* in the above article.

3. Define Pasteur effect. How they are correlated? Explain.

Refer article 15.4

4. Write an essay on fermentation.

Refer article 15.5

5. Discuss briefly the energy transfer system in respiration.

Refer *electron transport system* in article 15.6

6. What are the intermediate compounds formed in the breakdown of sugar during anaerobic phase of respiration.

Refer article 15.6 (i) and (iii)

7. Give an account of the chemical reactions involved in aerobic respiration of higher plants.

Refer article 15.6 (i) and (ii)

8. Give an account of anaerobic respiration in plants. Mention its importance in the respiration of green plants. What are the enzymes involved in the process.

For first and last part refer article 15.6 (i) and (iii). For the last part refer article 15.13

9. What is a Krebs cycle? Mention its significance in the metabolism of plants.

Regarding definition refer first para of article 15.6 (ii)

For its significance refer article 15.11

10. How fermentation differs from anaerobic respiration? What are the points of similarities?

Refer article 15.12

11. Point out clearly the relation between aerobic and anaerobic respiration.

Refer article 15.12

12. Describe the steps of pentose phosphate pathway of sugar breakdown in plants. Comment on any alternative pathway for this process.

Refer topic *pentose phosphate pathway* in article 15.9

13. Describe the environmental factors affecting the rate of respiration. Discuss the role of light in the process.

Refer article 15.15

14. Give an account of organic acid metabolism in succulent plants. How does the RQ of the succulent leaves vary in light and darkness.

Refer article 15.17

15. Describe the chemical reaction involved in the oxidation of pyruvic acid.

Refer article 15.6 (ii)

16. State the significance of determining the values of RQ of plant organs. Indicate when the values become zero, less than unity and infinity.

Refer article 15.3

17. Discuss that Krebs cycle is a link between carbohydrate and nitrogen metabolism in plants.

Refer article 15.11

18. What is P/R ratio? Discuss its importance in plant metabolism. What should be the P/R ratio of a normal metabolizing plant.

Refer article 15.14

19. What do you mean by compensation point? Critically discuss its value in normal metabolism of plant.

Refer article 15.14

20. Is there any modified Krebs cycle? If so, critically discuss the cycle.

Refer topic *the glyoxylic acid cycle : a modified Krebs cycle* in article 15.8

21. What is meant by P/O ratio? How the values varies depending on substrate.

Refer topic *electron transport system* in article 15.7

Plant Growth Substances

The growth of the plant is a dynamic and much complex one, yet it is a strictly controlled process. It means that growth in different parts of the plant is an integrated and co-ordinated process. This co-ordination of growth in different parts of the plant involves some control mechanism. As a result of intensive studies over many years, it is now known that hormones play a vital role in the control of growth. The term "hormone"¹ was first used by animal physiologists, to refer to a substance which is produced in a particular secretory gland and transferred in the blood or lymph to another part of the body where they become active in a minute quantity. Plant hormones, however, differ in certain respects from the classical concept of hormone. In case of plant hormone we cannot always differentiate between the site of hormone synthesis and place of action, although there are evidences indicating their effects at sites away from the place of synthesis. Another difference is that the effect of animal hormones are rather specific, a plant hormone, however, can elicit a variety of responses depending upon the type of organ or tissue in which it is acting. For these reasons plant hormones have been referred to as "growth regulators" or "growth substances" or "growth hormones". According to Thimann (1948 ; '52) a hormone may be defined as "*an organic substance produced naturally in higher plants, controlling growth or other physiological functions at a site remote from its place of production and active in minute amounts.*"

The *hormones*—substances produced in one part of a plant and transported to another part where they exert their influence—are the well known *auxins*, *gibberellins* and *cytokinins* which promote growth and the newly discovered *abscisic acid* (*ABA*), otherwise known as *dormin* because of its ability to slow down plant growth. They are therefore known as "growth inhibitors". Finally, there is *ethylene*, which inhibits growth and has other effects such as promotion of fruit ripening.

In addition to these, several dozen other plant hormones have been proposed. Some of them are well established, others may be found to be of little importance. Several remain hypothetical because they have never been extracted from plants and identified chemically.

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¹ The term "hormone" means "I arouse to activity". It was first proposed by Hardy and applied by Bayliss and Starling (1904) in animal physiology.

Several of the proposed hormones are involved in reproductive development. One is *vernalin* which plays a role in the low temperature preconditioning that makes biennials grow tall and bloom in the second year of their life.

Perhaps the most extensively investigated reproductive hormone of plants is *florigen* which was proposed by a Russian botanist in 1936. The hormone is supposed to be produced in leaves and was transported to buds, causing them to develop into flower buds rather than leaf buds. Although several experiments provide support for the florigen concept, but florigen has never been extracted definitively from plants and also has not been identified chemically. It thus remains a hypothetical hormone (detail refer Chapter 19).

TABLE 11
Classification of plant hormones

NATURAL		ARTIFICIAL	POSTULATED
Indole hormone	Non-indole hormone	1. IPA 2. IBA 3. NAA 4. 2, 4-D 5. 2, 4, 5-T	1. Rhizocaline 2. Caulocaline 3. Phyllocaline 4. Florigen 5. Vernalin 6. Dormin
A. Auxin 1. IAA 2. Indole aceto-nitrile 3. Indole acetaldehyde B. Glucobrassicin	Nitrogenous 1. Cytokinins	Non-nitrogenous 1. Gibberellins	

The existence of hormones in plants, their isolation and chemical identification came from the early work of Charles and Francis Darwin (1880) through their studies on the bending of the coleoptiles of grasses and cereals by unilateral light and of Sachs (1882, '87, '98) who first showed the existence of minute amounts of various chemical substances in controlling form and development among plants. The idea of these earlier workers has been strongly supported by Boysen-Jensen (1910, '11, '13) in the *Avena* coleoptile test. He showed that some chemical substances diffuse out from the coleoptile tip and cause a phototropic curvature resulted from unilateral light. Boysen-Jensen's experiments have been further supported by Paal (1914, '19). A new impetus in this line came from the work of Went (1928) who showed that the hormones present in coleoptiles actually diffuse out of the tip and are responsible for cell elongation, in plants. This hormone has been termed as *auxin* from the Greek word "auxein" meaning 'to grow'. Thus within a period of fifty years the whole concept of plant hormones has been changed considerably through improved methods of extraction and quantitative assay.

16.1 Auxins—The name *auxins* was given to the growth hormone produced by the tip of a coleoptile (Fig. 16.1A). If the stem tip is decapitated the growth of the region below the cut end will slow down and will ultimately cease to grow (Fig. 16.1B). On replacing the decapitated tip, growth of the stem in length is renewed (Fig. 16.1C). If the tip is now placed on an agar block for several hours and the block containing sap from excised coleoptile tip is replaced on the decapitated tip, growth is, however, renewed (Fig.

16.1E). The replacement of a pure agar block (without any pretreatment with excised coleoptile tip) however, shows no sign of elongation of the stem (Fig. 16.1D). These sequences in the chemical determination of growth and development began from the classical work of Darwin (1881) and led him to discover the occurrence of plant growth hormones now called auxins.

The action of auxins was first demonstrated by Söding (1925) in the coleoptile of oats (*Avena sativa*). Subsequent study by Went (1928), Kögl, *et al* (1934), Thimann (1935) and others has also demonstrated auxins as growth hormones in their control over coleoptiles and stems but their role in stimulating growth of roots and fruits is less certain.

The action of auxins in stems is almost proportional with the concentration of auxins. The activity increases with the gradual increase of auxin concentration. The action of auxins on roots is however reverse. Growth rate of the root decreases with increase of auxin concentration.

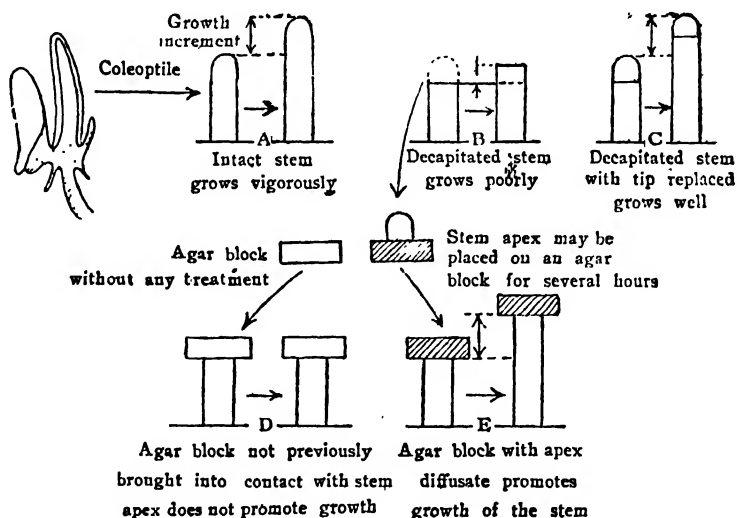


Fig. 16.1 Experiments demonstrating the production of growth-promoting substances by the stem apex.

Even the most sensitive chemical tests do not permit the accurate identification and measurement of small quantities of auxins present in plants. There are however, several biological tests by which the presence of auxins can be demonstrated. To measure the quantity of auxins in an unknown organ, the extract is applied to the coleoptile of *Avena sativa*, then the curvatures of the coleoptiles are measured. This curvature is then compared with the curvature produced by known quantity of auxins (Went, 1928). This technique of deter-

mining the quantity of chemical present in the extract from their response of an organism is known as *bioassay*¹.

A. CHEMICAL ASPECTS OF AUXIN—Kögl and Haagen-Smit (1931) first discovered the active principle of this growth hormone which has been termed as *auxin a*. The chemical identification shows that this substance is a nitrogen free compound known as auxenotriolic acid ($C_{18}H_{32}O_5$). Shortly afterwards Kögl, *et al* (1934) isolated another compound—auxenolonic acid ($C_{18}H_{30}O_4$) which they named as *auxin b*.

Both *auxin a* and *auxin b* are light and heat stable and can be easily oxidised. They can lose their activity gradually in a few months.

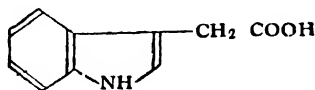


Fig. 16.2 Structural formula of β -indole acetic acid (IAA).

In the same year Kögl, *et al* discovered the third substance which they named as *hetero-auxin* whose chemical nature has been proved to be 3-indole acetic acid or IAA ($C_{10}H_9O_2N$). After its early isolation from yeasts (Kögl and Kostermans, 1931), *Rhizopus* sp. (Thimann, 1935) and from wheat and corn (Haagen-Smit, *et al* 1942, '46), it has now been isolated from a number of plants and is the most common and important plant hormone.

By the early part of 20th century the hormone concept thus becomes concrete with the extraction, isolation and identification of the active substance.

B. SYNTHETIC AUXINS—Of all three types of auxins, *auxin a* and *auxin b* are of rare occurrence while indole acetic acid (IAA) is almost universally present in all plants and is a major plant hormone. Besides these naturally occurring auxins there is a group of indole compounds which have the same formative effects as auxins (Kögl,

¹ Apart from the well known *Avena* test, mention may also be made of (a) Split Pea test (Went, 1934); (b) Straight growth test (Bonner, 1933); (c) Pea Root test (Fiedler, 1936); (d) Root inhibition test (Swanson, 1946); (e) Leaf repression test (Thompson, *et al* 1946); (f) Tomato ovary test (Luckwill, 1948) and (g) Ferric chloride test (Tang & Bonner, 1947; Gordon & Weber, 1951). For all tests refer Leopold's *auxin and plant growth*, 1955).

Besides, the chromatographic separation and identification has proved a successful and valuable means for separating and identification of growth substances. The main technique for chromatographic separation of auxins is by partition between two liquid phases—one stationary and the other mobile—cellulose acting as an inert support. Since different substances move at different rates, the separation is effected depending on their distribution ratios of the solvents. The R_f values (the ratios of the distance traversed by a substance to that traversed by the solvent front) and colour detection methods have been proved successful for detecting indole derivatives (Sen & Leopold, 1954).

et al 1934, Haagen-Smit and Went 1935, Zimmerman, 1936). A number of phenoxy acetic acid derivatives is found to be equally important in causing formative effect on plants. Among them α -naphthalene acetic acid (NAA) was observed by Zimmerman, *et al* (1936) and β -naphthoxy acetic acids by Irvine (1938), Zimmerman and Hitchcock (1941). The ability of benzoic acid to produce growth and formative effect has been demonstrated by Bentley (1950).

Phenoxyacetic acid also stimulates the growth of plants like auxins. The best example of which is 2, 4-dichlorophenoxy acetic acid (2, 4-D), a highly active auxin.

C. AUXIN BIOSYNTHESIS—The pathway of auxin synthesis in living plant cells involves a series of steps, all of which originate from the amino acid tryptophan, a compound with an indole nucleus which is universally present in plant tissues (Wildman, *et al* 1947). The general path in the synthesis of auxin is the formation of indole pyruvic acid, an intermediate by oxidative decamination. The conversion may involve the formation of tryptamine by decarboxylation. In both the cases IAA is formed via indole-3-acetaldehyde, where a number of oxidative enzymes may complete the final conversion to indole acetic acid (Gordon, 1961).

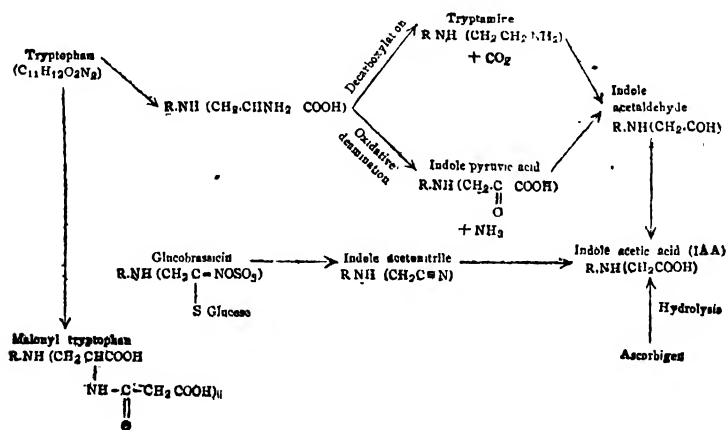


Fig. 16.3 Possible biosynthetic pathways for indole acetic acid (IAA) in plants.

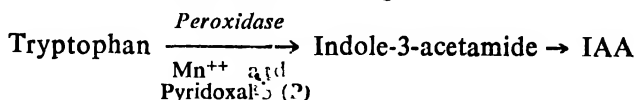
IAA may be formed from nitrile compound (indole-3-acetonitrile) by *nitrilase* (Thimann and Mahadevan, 1958). This nitrile compound is formed from glucobrassicin (Gmelin and Virtanen, 1961; '62).

IAA may also be formed from ascorbigen (another glycoside) on hydrolysis (Kutacek, *et al* 1960). The whole scheme of auxin synthesis is shown in Fig. 16.3.

Tryptophan may be converted to malonyl tryptophan and thus blocking the auxin synthesis (Lenk, 1963).

Synthesis of auxin is mainly affected by the types of tissues, light intensities and by zinc. Deficiency of zinc will prevent auxin formation by retarding the synthesis of tryptophan—the auxin precursor.

Riddle and Mazelis (1964) showed that the synthesis of IAA proceeds according to the following scheme.



Apart from the indole compounds shown in Fig 16.3 regarding the synthesis of IAA, a number of other indoles are known to occur naturally in plants. It is possible that any one or all of these indoles could serve as precursor of IAA synthesis, but actual details are not known.

D. SITES OF AUXIN SYNTHESIS AND THEIR OCCURRENCE—The auxins are therefore the metabolic products of plants and are universally present in all plants. The usual sites of auxin synthesis in vascular plants are the apical meristems and enlarging tissues. The classic demonstration of hormone synthesis in the apex of grass coleoptile by Darwin (1897) and further elaborated by Paal (1919) was experimentally proved by Went (1928).

Auxin which is synthesized at the apex of the stems moves downwards and provides the stimulus for growth in the regions below the tip of the stem. The concentration of auxins is not the same in all tissues. The greatest quantities of auxins are present in seeds or structures pertaining to seeds, in stem tips and in young expanding leaves (Lecopold, 1955).

The investigations of various workers have demonstrated the important variants of this situation regarding the occurrence of auxins in plants. Thus Mirov (1941) has shown that in pine shoot the auxin concentration is greater at basal part than the apical region. Similar observation has been made by Gunckel and Thimann (1949) in the internodes of *Ginkgo*.

The enlarging of the leaves of higher plants is related with the production of more auxin although its effects on the leaf blade are generally small (Miller, 1951 ; Kuraishi, 1959).

In plants auxins generally exist in two forms viz. *free* and *bound auxins*.

(a) *Free auxin*—the portion readily available by diffusion or rapid extraction is capable of moving freely in the polar transport system being apparently immediately effective in growth.

(b) *Bound auxin*—the portion available after enzyme action, hydrolysis or extraction extended over a longer period of time. According to Larsen (1951) bound auxin may exist as an auxin-protein complex, natural precursors of auxins, precursor complexes and structural protein sources of auxin. From this auxin-protein complex,

active auxins can be released then the bound auxins are referred to as auxin precursor. These forms of auxins account for the total auxin concentration in plant cells.

E. AUXIN TRANSPORT—Since the site of auxin synthesis and the regions of auxin action are quite different, it must be translocated from the site of synthesis to its region of action. This transport of auxin is typically a *polar transport* (i.e. it moves only basipetally). The basipetal movement of auxin has been experimentally proved by Went (1935). At the morphological upper end (A) of the *Avena* coleoptile if an agar block containing auxin is affixed and an ordinary pure agar block is placed at the morphological base (B) irrespective of the orientation of the tissues with respect to gravity (Fig. 16.4I) auxin is found to be moving from morphological apex (A) to the base (B) through the parenchyma cells of the coleoptile and will gradually accumulate in base (B). No such movement of auxins will take place if blocks are placed in a reversed condition i.e. the block containing the auxin at the morphological base and ordinary agar block at its apex (Fig. 16.4II).

Polar transport is very active near the stem or coleoptile tips and it gradually declines with the distance down the plant (Van der Weij, 1932 ; Jacobs, 1950).

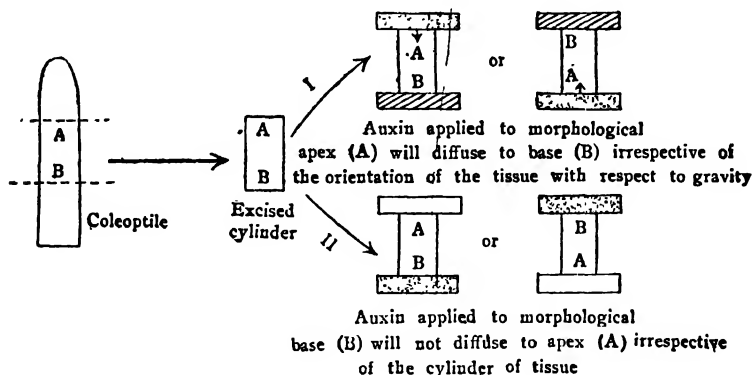


Fig. 16.4 Experiment demonstrating the flow of auxin through coleoptile tissue.

A more or less erratic transport has been observed in the root and both upward and downward movements have been observed in many older roots (Gorter, 1932). Where the auxin is mixed up with the transpiration stream or it is applied to the roots or basal part of the plant, upward movements of auxin can be demonstrated (Hitchcock and Zimmerman, 1935 ; '38). In the upward movement, as soon as the auxin molecules come in contact with the living tissues their characteristic polarity is resumed (Skoog, 1938).

The velocity of the polar transport of auxin lies between 0.5 cm and 1.5 cm per hour.

F. MECHANISM OF AUXIN ACTION—The problem how a minute amount of hormone (auxin) can bring about such dramatic change in the growth of the plant is one of the interesting and biologically challenging problems in plant physiology.

Several theories have been proposed on the mechanism of hormone action which may be summed up in the following sections.

(a) *Hypothesis of osmotic effect*—The ultimate effect of growth by cell enlargement is caused due to the enlargement of the protoplast by water uptake. Thus the auxin softens the cell wall by increasing its plasticity (Heyn, 1931; Tagawa and Bonner, 1957; Cleland, 1958) which ensures the swelling of the wall by simple osmotic water uptake.

In 1931, Heyn showed that auxins cause a softening of the cell wall. Since the cell walls are cemented together by pectin chains made firm by calcium, this Ca-linkage must be removed to ensure the softening of the cell wall and to cause growth. Thus the effect of auxin in removing calcium linkage has been suggested by Bennet-Clark (1956) and the site of the Ca-linkage is the main region of auxin attack. In 1960 Masuda suggested that auxin brings about an increase in the available RNA which binds Ca-ions, thus making them less effective in cementing the cell walls of the plant cells.

Besides cell plasticization auxin can cause the synthesis of new cell wall materials. Thus it has been observed by Christiansen and Thimann (1950) that in pea, auxin treatment causes the accumulation of cellulose and hemi-cellulose. This idea of cell wall synthesis as a basic growth stimulus by auxin is however overturned by Bennet-Clark (1956), Ordin and Bonner (1957) and others.

(b) *Hypothesis of enzyme effect*—It has been found by various workers that by the addition of hormone there is an increase in the enzymatic activity within the cell.

Northern (1942) found that hormones caused a decrease in the cytoplasmic viscosity and at the same time brought about dissociation of protein constituents of the cytoplasm. This dissociation activates the enzymes particularly in increasing the availability of the substrate for the enzyme. As a result of this, respiratory activity increases and consequently growth might follow.

Another enzymatic mechanism of auxin action has been proposed by Thimann (1951) who showed that sulfhydryl containing enzymes are very much related with growth. According to him the auxin acts not as enzyme activating agent but as agent protecting auxin from inactivation.

(c) *Molecular reaction hypothesis*—Skoog, *et al* (1942), Foster, *et al* (1962) and many others approached this problem from different points of view and suggested that auxin may act by attaching to

some entity (enzymatic) of the cell. Thus according to them auxin acts as a sort of co-enzyme.

Thus the mysterious problem of auxin action still remains unsolved though several hypotheses have been put forwarded to explain this mechanism. The concept that auxin softens the cell wall which

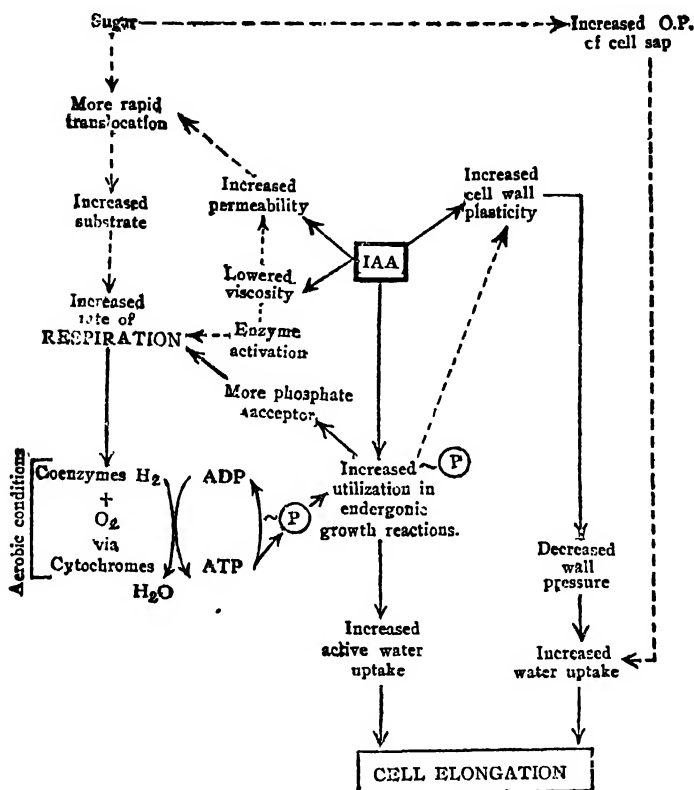


Fig. 16.5 Interrelations between the possible modes of auxin action (modified after Strafford, 1965).

permits easy water uptake and expansion of the cell wall is very attractive. But it is still a matter of controversy as to how this action may be related to changes in pectic or other structural components of the cell wall.

The mode of auxin action have been shown in Fig. 16.5.

G. ROLE OF AUXINS :

(a) *On growth*—The action of auxins in controlling growth appears to be a complex of many functions. Since the early work of Went (1928), a large number of workers in recent years have come to

the conclusion that no growth is possible without auxin. The relative sensitivity to auxins of different plant organs has been shown by Boysen-Jensen (1936). According to him roots have a much higher sensitivity to auxin and they can be stimulated to growth at a much lower concentration than stems.

The role of auxins is to both stimulate and inhibit the various growth functions of plants. They can promote or inhibit the differentiation of buds, production of flowers, abscission, activity of certain enzymes etc. and in all these cases, the effect obtained is due to effective auxin action in the tissues. (For details refer topic *mechanism of auxin action*).

(b) *On tropism and movement*—The effect of auxin in tropism and plant movements has been effectively carried out on the curvature of *Avena* coleoptiles.

It has been independently worked out by Cholodny (1927) and Went (1928) that unequal distribution of auxin was responsible for the bending of plants towards light. The unequal distribution of auxin is due to light-induced lateral distribution of auxin (For details refer Chapter 20 article 20.2(i)).

Another cause of phototropic curvature is reaction of light on growing cells. Light causes a desensitization of growing cells to a given amount of auxin (Galston and Baker, 1953), but the actual relationship has however not been established.

Other factor of phototropic curvature is the destruction of auxin by light and thus under lighted condition auxin destruction on the lighted side will cause curvature towards the light.

Since the photo-destruction of auxin is a chemical reaction induced by light, it (light) must be absorbed by some plant pigments. According to Wald and DuBois (1936), β -carotene and according to Galston (1949), riboflavin is the photoperiodic pigment responsible for the photo-destruction of auxin.

Like phototropism, auxins have a pronounced effect on geotropism. As in phototropism, geotropism is also due to lateral distribution of auxin by gravitational forces (Dolk, 1929). Due to gravitational force nearly 60% of auxin appear on the lower side of root tip or stem. This asymmetrical distribution of auxin causes an asymmetrical growth—stems bending away from the gravitational force and roots towards it (as roots are more sensitive to auxin action at a lower concentration than stems).

Another possible explanation of geotropism has been made by van Overbeek, *et al* (1945), who showed that more auxin formation takes place in meristems just above each node after it has been subjected to geotropic stimulation. So in horizontal position auxin is synthesized on the lower side and consequently more activated.

A similar type of tropic movement (e.g., thigmotropism) has also been discussed by Went and Thimann (1937).

(c) *Inhibition effects*—Thimann and Skoog (1933) first demonstrated that apex is the main source of auxin for the plant and its removal results in the loss of apical dominance and stimulates the development of lateral buds. So the presence of larger amount of auxin in the apex favours the development of an unbranched plant form whereas plants with low auxin concentrations develop a branching habit.

As the auxin concentration in a plant is the primary factor in the inhibition of lateral buds, treatments like irradiation, injection of dyes in the light etc. which reduce the auxin level will stimulate branching (Chailakhyan and Zdanova, 1933 ; Leopold, 1949).

Branching in roots also involves an auxin mechanism similar to shoots, as decapitation of the roots can cause branching.

(d) *Organ differentiation*—Auxins and other plant hormones not only affect growth by elongation, but also affect the morphological type of growth. Thus by applying auxins a young stem may develop cluster of cells differentiated into callus, roots, vegetative buds and sometimes even flowers. Like other auxin effects, a dualism is exerted in the control of organ differentiation. A relatively high concentration of auxin causes dedifferentiation of tissues which result in the formation of callus. Whereas under certain circumstances, auxin can redifferentiate these callus or meristems into roots, buds or flowers.

(e) *Fruit development*—The role of auxin in the normal process of fruit-set without pollination (parthenocarpic fruit-set) has been thoroughly investigated by Gustafson (1936). This discovery of fruit-set by auxin treatment has a great value in commercial practice in producing fruit-set when natural set is difficult.

To find out the actual cause of fruit-set by auxin treatment is a difficult problem and it might be due to either "incitement of growth of the young fruit" or due to prevention of abscission of the flower.

(f) *Abscission*—In most plant species there comes a time during the life of each leaf and fruit when they shed from stem. The process by which leaves and other organs such as fruits and flowers are removed from the plant is known as *abscission*. It is due to formation of a *separation* or *abscission layer* at the base of the petiole. It is like thin plate of cells oriented at right angles to the axis of the petiole. The wall of the separation layer become softened and gelatinous, forming a weak region which readily break under slight strain.

Formation of separation layer is related to a fall in the auxin content. As the organs get older their auxin content declines and consequence is the formation of separation layer. The use of synthetic hormones in the abscission of leaf has been pointed out by LaRue (1939) and later on its role in the control of abscission of petioles, flowers and fruits has also been pointed out.

The auxin action on abscission has been experimentally proved by Addicott and Lynch (1951). The effect of its action depends on the locus of its application. Auxin applied to the distal cut end of a petiole after removal of auxin-synthesizing lamina delays abscission of the petiole; whereas when it is applied on proximal side (stem) it has an opposite effect i.e., abscission is accelerated rather than delayed by auxin.

The role of the auxins in the developmental functions of fruit-set, fruit size and in the control of abscission has been discussed in article 16.4.

H. AUXIN INACTIVATION—Inactivation is almost synonymous with ‘destruction,’ but it means only the “loss of biological activity in a chemically determined manner”. Inactivation of auxin is a normal phenomenon in plant life. Early experiment of Went (1928) with exposure of *Avena* coleoptile to light indicates the reduction in the amount of auxin present. This led Tang and Bonner (1947), Galston (1949) and others to suggest that the light-activated processes—enzymatic and non-enzymatic—can inactivate auxin in plants. Photo-activation of auxin is chiefly due to the presence of photodynamic compounds like riboflavin, methylene blue etc. (Gordon, 1954). The detail account of auxin destruction has been made by Larsen in 1951. The whole scheme has been represented in Fig. 16.6.

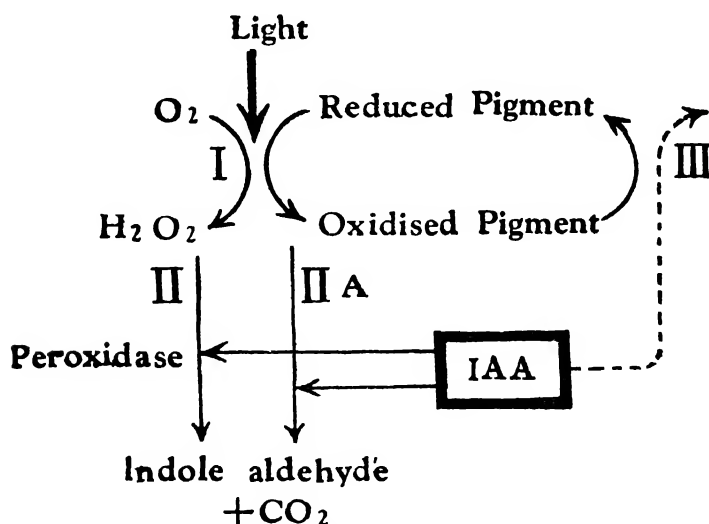


Fig. 16.6 Possible scheme for auxin inactivation.

In this scheme reduced pigment (flavo-protein complex) is first oxidised by oxygen and forms peroxide (I). Next stage is an enzymatic reaction leading ultimately to the destruction of auxin. The

enzyme involved is a *peroxidase*. As a result of this reaction indole acetic acid (auxin) is oxidised to indole aldehyde and carbon dioxide (II). Another alternative reaction of the destruction of IAA is a non-enzymatic one where IAA is oxidised without the participation of an enzyme (IIA). Possibly a second non-enzymatic destruction of auxin proceed (III) in the regeneration of the original reduced pigment (flavo-protein).

Regarding the effect of light in the enzymatic reaction Galston and Baker (1951) showed that there is a natural inhibitor in pea and activity of this inhibitor can be overcome by light, causing the destruction of auxin. Light therefore acts to prevent the effect of the inhibitor on the enzymatic destruction of auxin.

The nature of enzyme responsible for auxin destruction is also a matter of dispute. It may be either an iron-enzyme (*cytochrome oxidase*) or a *peroxidase*.

The ultimate products of the auxin destruction are indole aldehyde and carbon dioxide in both the enzymatic (II) and the non-enzymatic (IIA) destruction (refer Fig. 16.6).

Auxin inactivation in plants may be due to formation of hormonally-inert complexes of various types. Thus IAA can readily be esterified by plant enzymes to form indole ethyl acetate or with amino acid to form indole-acetyl-aspartic acid. IAA also forms conjugates with various sugars and sugar-alcohols.

Auxin destruction can also be made by increasing pH of the medium, X-ray and heat treatment.

16.2 Gibberellins—At about the same time when the proper status of auxin as one of the most important constituents of plant cell has been established, work in Japan produced another biologically active substance known as *gibberellin*. It has been observed by Japanese plant pathologist Kurosawa (1926) that a soil borne disease known as “bakanae” disease of rice caused by *Gibberella fujikuroi* was responsible for extensive growth of the infected rice plants. He further showed that the cell free extracts of the fungus applied on healthy rice seedlings caused elongation, a symptom characteristic of the disease. Metabolic product of this fungus therefore was responsible for the enhanced growth. This active principle has been named *gibberellin* by Yabuta (1935). Subsequent work by Brian in England and Stodola in the U.S.A. has resulted in the discovery of 3 related active compounds—gibberellin A₁, gibberellin A₂ and gibberellic acid (GA₃). So far forty different gibberellins have been isolated and characterised. Of all known gibberellins, GA₃ is formed in greater amount than other gibberellins and detailed study as regards their chemistry and physiological activity has been carried out most extensively.

A. Chemistry of gibberellins—The detailed study regarding the structure of the gibberellins has mainly centered round the work of

a number of workers (Cross, *et al* 1961 ; MacMillan, *et al* 1961) According to them gibberellins are colourless aliphatic acids and are 5-ringed diterpenoids. Analytical study shows the empirical formula for the GA_3 to be $C_{19}H_{22}O_6$ (Cross, 1954).

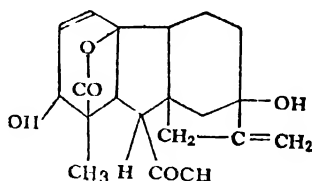


Fig. 16.7 Structural formula of gibberellic acid (GA_3).

All gibberellins have the same basic molecular structure (the gibbane-carbon 'skeleton') as gibberellic acid, differing from one another mainly in the number and positions of substituent groups on the ring system and the degree of saturation in the 'A' ring.

B. *Biosynthesis of gibberellins*—All terpenoids are basically built up from "isoprene units", which are five-carbon compounds. The linking of two isoprene units yields a monoterpene ($C=10$), of three a sesquiterpene ($C=15$) and of four a diterpene ($C=20$). The question of biosynthesis of gibberellins is still a debatable one. However the work of Birch, *et al* (1958) with redioactive isotope suggests a possible pathway that might lead to the synthesis of

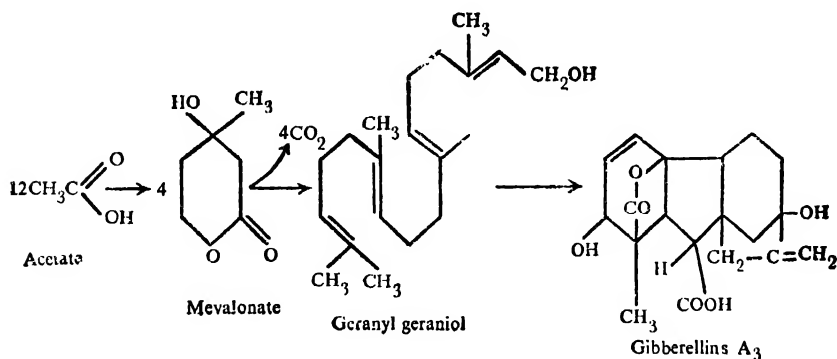


Fig. 16.8 Proposed route for the biosynthesis of gibberellic acid (GA_3).

gibberellins. The possible precursor of the gibberellins is a two carbon compound, acetate. By labelling the carbon atom (^{14}C) of the carboxyl group of the acetate. Birch, *et al* (1958) observed that gibberellic acid (GA_3) is synthesized via mevalonate and geranylgeraniol. The whole scheme of the synthesis of gibberellic acid is given below (Fig. 16.8).

C. *Occurrence of gibberellins*—Most of the workers (West and Phinney, 1958) believe that gibberellins occur naturally in the plants. According to Corcoran and Phinney (1962), most of the gibberellins occur in maturing seeds particularly involved in the seed maturation processes. Gibberellins are also present in the germinating seedlings (Wheeler, 1960) and are said to be abundant in the growing tissues such as expanding cotyledon or leaf.

Gibberellins occur in plants either in bound or modified form.

D. *Role of gibberellins*—The effectiveness of gibberellins in regulating growth and quantitative change in growing tissues suggests that they are the natural growth regulating systems in higher plants. They are also involved in some types of dwarfism of the plants particularly in the growth elongation of dwarf corn, dwarf pea and elongation of rice seedlings. The first successful assay using dwarf corn was made by Phinney, *et al* (1957) and later on with dwarf pea (McComb and Carr, 1958), and rice seedling (Hashimoto and Yamaki, 1960).

Besides their role in dwarfism, the gibberellins are also involved in the phenomena of dormancy, flowering and fruiting. That gibberellins are related with dormancy of plants has been shown by Kahn, *et al* (1957) and there is an increased accumulation of gibberellins when the seeds emerge from the dormant condition (Naylor and Simpson, 1961). Gibberellins can induce flowering in the photoperiodically sensitive plants (Lang, 1956). Gibberellins have a definite role in the sex expression in Cucurbitaceae [Mitchell, *et al* (1962)]. Gibberellins cause formation of male flowers whereas low concentration of gibberellins favours the formation of female flowers. Gibberellins can also effectively control fruit-set within the plant (Gustafson, 1960).

Gibberellins, however, on the other hand, can suppress both bud and root formation (Murashige, 1961).

In germinating seeds the embryos produce gibberellins and these diffuse into the endosperm where they induce the synthesis of α -amylase and other hydrolytic enzymes (e.g. proteases), thus bringing about digestion of the foods in the endosperm. If the embryo is excised from the seeds, these enzymes are not produced unless gibberellins are supplied to the endosperm. There is evidence that the gibberellin acts by inducing the production of new kinds of mRNA that code for the enzymes. Whether or not this is the way gibberellins act in all cases where they promote growth is not known.

Gibberellins thus appear to influence many fundamental physiological processes in addition to growth elongation, but to little experimental work has been done yet to ensure whether their effects are general or are merely anomalous individual effects.

E. *Mode of action of gibberellins*—Gibberellins, which when applied externally can make a dwarf plant grow to normal size, are also involved in cell enlargement. The way in which gibberellins

affect the cell wall is much less clear than auxins. It has been suggested that gibberellins act by altering the concentration of auxin in plant stems so that they indirectly affect wall extensibility. Cleland *et al*, however, have shown that in cucumber seedlings IAA and gibberellic acid have clearly different effects on the cell wall. It is of course possible that gibberellins affect the behaviour of auxins in other plants. Perhaps in cucumber, gibberellins promote growth by increasing the osmotic concentration of cell sap, so that water enters the cells and swells them. This is the credible explanation because gibberellins have already been found to increase the concentration of hydrostatic and proteolytic enzymes in plant cells.

F. *Gibberellins and auxins*—Cell extension which is mainly controlled by auxins, particularly IAA (Audus, 1955) has also been found to be controlled by one of the best known gibberellins—gibberellic acid; but the detailed study of the physiological properties of gibberellic acid and indole acetic acid reveals some interesting differences.

IAA induces the extension of etiolated coleoptiles and the growth response curve shows a linear elongation within the range of 0.01—1.00 $\mu\text{g/ml}$. GA however shows very little elongation of the coleoptile tip.

Auxins in addition to their effect on cell extension cause cell division—GA₃ however does not have any such effect on cell division. Thus treatment of cuttings with auxin helps in the initiation of roots. GA₃ antagonizes such root formation.

When auxins are applied on the decapitated tip of the main shoot, development of laterals is inhibited. GA₃ stimulates more rapid development of the laterals.

Auxins normally inhibit leaf abscission and produce abnormal cell proliferation in some tissues. GA₃, however, has no such effect.

All these differences between auxins and gibberellins lead naturally to assume that these two substances must act differently. But Brian, *et al* (1957) show that in producing their effect they must act similarly and so GA₃ depends for activity on the presence of IAA, although the effects of these two are complimentary.

16.3 Cytokinins—That gibberellins and auxins can only stimulate cell enlargement has been clearly pointed out in the preceding articles. The need for the existence of a control system for cell division led many (Wiesner, 1892; Haberlandt, 1913 and others) to suggest diverse types of chemicals present for cell division effect. Thus in 1956, Miller, *et al* first isolated from yeast DNA a group of active substances which can stimulate cell division and these have been named as kinetin.

Cytokinins usually seem to influence plant growth by stimulating cells to divide, although in some tissues they affect only cell enlargement. Another more spectacular property of cytokinins is their

ability to induce the formation of organs by undifferentiated plant tissues. The effects of cytokinins in combination with auxins have given some indication of how these two groups of substances can interact and suggests some ways in which they might interact in the whole plant

By varying the concentration of kinetin in a constant amount of IAA, Skoog, *et al* were able to induce undifferentiated tobacco callus tissue. In the absense of kinetin or in the presence of too high a concentration there was little or no growth. With low concentration of kinetin roots developed and with relatively more kinetin, buds developed. When intermediate concentrations were present, however, the undifferentiated callus continued to grow unchanged.

Since this early work in the 1950, a great deal of information has accumulated about the effect of auxins and cytokinins on plant growth. In herbaceous plants there is a general tendency for callus cultures to produce shoots when provided with high ratio of cytokinins to auxin and to produce roots when the ratio is low.

These experiments have shown that plant growth clearly involves close interaction between different growth promoting substances. In various combinations and concentration they can set in motion the different processes of development.

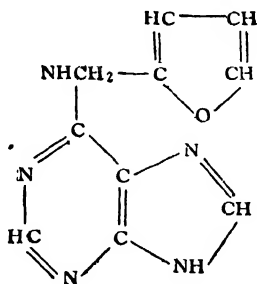


Fig. 16.9 Structural formula of kinetin (6-furfuryl amino purine).

The chemical study of kinetin strongly suggests that it is a 6-furfuryl amino purine basically similar in structure to adenine (Fig. 16.9).

Majority of the kinins have been isolated from fruits and endosperm tissues. Coconut milk is the richest source of kinins (Steward and Capline, 1952). Kinins have been successfully isolated from a number of fruits like apple, tomato, plum, banana etc. More recently, Skoog (1963) showed the presence of kinins in the vegetative tissues.

The first naturally occurring cytokinin called *zeatin* was isolated from maize kernels. To date eight cytokinins have been found in maize kernel extracts.

Kinins cause changes in the protein and nucleic acid components of tissues which are the basis of the kinin effects on cell division (Guttaman, 1956) as well as on growth and mobilization actions. Cytokinins bring about the mobilization of various solutes including amino acids, auxin and phosphorus. They also delay the senescence of leaves particularly detached one when it applied to the leaves. This is at least partly a result of their mobilizing effect. When leaves are detached there is extensive hydrolysis of proteins and RNA and translocation of amino acids, mineral salts and other solutes out of the leaves. Cytokinins apparently promote the synthesis of protein, RNA and other essential substances and also reducing translocation of such solutes out of the leaves because of their mobilizing influence.

The most important differences between the kinins and the other growth substances are that kinins are not acidic in reaction like auxins and gibberellins. It has been found by Woolley (1957), that plant hormones are more acidic because of the acidic nature of the plant cell walls; the alkaline materials are less mobile and kinins are the extreme case of non-mobility because of their non-acidic reaction.

16.4 Role of hormones in agriculture and horticulture :—There is a large number of synthetic organic compounds which when applied to plants bring about some responses which are indistinguishable from those of naturally occurring hormones. The classical role of these synthetic hormones initiated the entrance of growth substance into the field of agriculture. During the last 30 years the role of these hormones in the form of growth regulations has been extensively worked out. All these synthetic hormones are effective in a very low concentration. Low concentration and low cost of production are the important criteria in the use of these plant hormones (both natural and synthetic) in agriculture and horticulture.

A. EFFECTS ON VEGETATIVE PLANT STRUCTURES :

(i) *Role in the rooting of cuttings*—Extensive trials have been carried out to determine whether the promotion of rooting by traces of auxins and of synthetic substances has any possible horticultural application in the propagation of plants by cuttings. Several successes have been achieved since the work of Sachs (1880-1893), van der Lek (1925), Went (1929) and lately of Thimann and Went (1934) who showed the root forming activity of auxins. In 1935, Thimann and Keopfli showed that IAA can stimulate root formation. So, it can be said safely that the hormones enter into the complex reaction system that initiates the pericyclic division and ultimately the formation of root primordia.

Besides IAA, IBA (indole butyric acid), NAA (naphthalene acetic acid) etc. are the best known hormones which can rank high from the standpoint of general usefulness.

The importance of such horticultural practice of propagation by vegetative method is far reaching. By means of such cuttings a great many identical plants may be obtained from a single individual and a number of desired genetic pattern may be preserved, generation after generation.

(ii) *Role in controlling cambial activity*—In woody plants continued increase in girth of stem and root takes place by the activity of cambium. The activity of cambium is highest in spring and it declines in summer and it accounts for the formation of annual rings in such trees. This rhythm of cambial activity is intimately linked with the hormone (IAA) as it was very effective in stimulating meristematic activity in the cambium (Snow, 1933).

(iii) *Role in the formation of callus and healing of wounds*—Another important function of cambium is the formation of callus or wound tissues and the healing of wounds.

During pruning of plants there is a possibility of infection by some pathogenic organism in the wound area. In order to overcome such infection some substances are found to have oozed out of the wounded cells which cause the surrounding uninjured cells to become meristematic resulting in the formation of *wound tissue* or *callus*. Hormones are found to be very effective in stimulating callus formation thus healing the tree after pruning operation. Such effect has been shown by Shear (1936) in the application of 1% IAA to cause stimulation of wound healing of peach, plum, apple etc.

(iv) *Control of undesirable plants or weed control*—One of the most spectacular uses of synthetic hormones is to use them against the most old enemy of agriculturists and horticulturists, the weeds.

In killing weeds synthetic hormones have got a number of advantages: (a) the hormones which are used as herbicides are highly selective, affecting only the broad-leaved plants whereas the grasses are relatively resistant. Since majority of the weeds are broad-leaved, these hormones can be effectively useful under many conditions; (b) they are non-toxic and non-corrosive to animals and human beings in the concentration used to kill weeds; (c) they are effective at a very low concentration and hence they are inexpensive; (d) their effect on the soil is not permanent and (e) they can be effective through soil and foliage.

The herbicide 2,4 dichlorophenoxy acetic acid (2, 4-D) has proved to be an ideal weed killer. 2-methyl, 4-chlorophenoxy acetic acid (MCPA) and 2, 4, 5-trichlorophenoxy acetic acid (2,4, 5-T) are also used frequently for their selectivity.

The most effective way of applying these herbicide is in an aqueous spray on the foliage. Generally a concentration of 0.1% (at rate 5 gallons/1000 sq feet) considered to be the standard strength, is applied to the plants.

The dosage of hormones, the time of application and the environmental factors are the important criteria of hormone action. Temperature, sunlight and rainfall are also the influencing factors of hormone effect.

(v) *Role in the prevention of sprouting of potato tubers*—Early break of dormancy of potato tubers is a source of trouble to the agriculturists as it can cause rapid loss of weight and decrease in the starch content of the tubers. It has been found by Guthrie (1938) that by dipping potato tubers in IAA solution sprouting of potatoes can be inhibited. Similar effect can be obtained by the application of methyl α -naphthlene acetate for effective inhibition of buds of potato tubers (Guthrie, 1939).

B. EFFECT ON THE REPRODUCTIVE STRUCTURES OF PLANTS :

(i) *Control of floral initiation*—The idea that flowering might be controlled by a hormonal stimulus was suggested by Sachs (1882) and later on corroborated by more recent findings of Cajlachjan (1935) and Moskov (1936). The first demonstration that hormone could initiate flowering was made by Hitchcock and Zimmerman (1935). The study that synthetic hormones could favourably initiate flower formation, was made by Clark and Kerns (1942). They showed that a very low concentration of NAA (naphthalene acetic acid) over vegetative bud of pineapple caused the formation of flower bud 2, 4-D also can favourably initiate flowering (van Overbeek, 1945).

More recently, gibberellins have been shown to induce flower formation of some photoperiodically sensitive and some cold-requiring plants like *Hyoscyamus* and *Samolus* (Lang, 1956, Lang, *et al* 1957).

(ii) *Control of fruit development (parthenocarpy)*—Although attempts have been made since a long time to produce parthenocarpic fruits (i.e. to produce fruits without fertilization), no tangible results were obtained until 1936 when Gustafson induced parthenocarpic development of fruits (i.e. seedless fruit) in tomato, squash, pepper, *Petunia* and other species of plants by the application of IAA and IBA. α -naphthalene acetic acid has also been subsequently found to produce parthenocarpic fruits in strawberry (Gardner and Marth, 1937).

Since then a large number of chemical substances have been tested for their capacity to induce parthenocarpy. Among the derivatives of indole, indole butyric acid (IBA) appears to be the most effective. Derivatives of naphthalene (α -naphthalene acetic acid and β -naphthoxy acetic acid) are also equally important for the induction of parthenocarpic fruits.

(iii) *Role in the inhibition of abscission layers*—Abscission is a common phenomenon in plants ; the shedding of leaves and of entire flowers or part of flowers, dropping of fruits are the familiar examples of abscission.

Using auxin from orchid pollinia, Laibach (1933) was the first to observe hormonal control of abscission. Gardner, *et al* (1939) reported that abscission could be delayed by spraying with synthetic plant hormones.

Preharvest drop of fruits results in serious reduction in yield of fruits and so the use of synthetic hormones in controlling the preharvest drop is one of the most useful and economically important aspects in horticulture. This is true for a number of fruits, such as apples, pears, plums, peaches, oranges etc.

Among the synthetic hormones 2,4-D, NAA or naphthalene acetamide have been found to give the best results. To be effective, these hormones must be applied during or before the dropping is well started. Studies on the promotive and inhibitory effects of various auxin concentrations led Leopold (1958) to suggest that abscission has a two-phase response. In one hand they can delay abscission, on the other hand they can also hasten it, depending upon concentration and place of application.

(iv) *Role in thinning of blossom and control of fruit production*—Within the past few years chemical sprays that can reduce fruit set by pilling some of the flowers have been discovered; thus accomplishing both fruit thinning and more even yearly bearing. Although this work is still in the experimental state but it can promise an important contribution in the blossom thinning of cherries, peaches and apples.

(v) *Role in the fruit growth and maturation*—Plant hormones can be effectively applied in the control of size and maturation of fruits. Thus Howlett *et al* (1941; '48) first reported that application of IBA to the flowers of tomato plant stimulates fruit growth. Wiltwer and Murneek (1946) also showed the stimulation of fruit growth by the application of 4-chlorophenoxy acetic acid and other phenoxy compounds in snap bean. In their experiment not only the maturation of fruits was hastened but the final size was also increased. Similar effect was also obtained by 2, 4, 5-trichlorophenoxy acetic acid in peach fruit (Marth and Haris, 1950).

The exact knowledge as to how these growth regulating substances affect the various metabolic process of fruits so as to stimulate their growth and hasten their ripening is a matter of controversy. Any way, that they can hasten the maturity is more or less certain.

SELECTED QUESTIONS

1. Write a historical development of auxins. Explain the phenomenon of the hormone concept.

Refer introductory part of Chapter 16

2. Define auxins. Write an essay on their detection and bioassay.

Refer article 16.1

3. Give a detail account of chemical nature of auxins. Discuss the distribution of auxins in plants.

Refer *chemical aspects of auxins* and *sites of auxins synthesis and their occurrence* in article 16.1A and 16.1D

4. Write what you know about the biogenesis of auxins. Give a critical appraisal of tryptophan as a primary precursor in the synthesis of auxins.

Refer *synthesis of auxins* in article 16.1C

5. How auxins can be transported in plants.

Refer *auxin transport* in article 16.1E

6. Discuss critically the theories of mechanism of auxin action in plants.

Refer *mechanism of auxin action* in article 16.1F

7. What are gibberellins ? Discuss the role of gibberellins in plants.

Refer article 16.2 and the topic *role of gibberellins* in article 16.2D

8. Write an essay on the history of discovery of gibberellins. How they can be distinguished from the auxins.

Refer article 16.2 and the topic *gibberellins and auxins* in article 16.2F

9. Discuss the occurrence, chemistry and role of gibberellins.

Refer topics *occurrence of gibberellins*, *chemistry of gibberellins* and *role of gibberellins* in article 16.2C, 16.2A and 16.2D respectively.

10. Write an essay on cytokinins.

Refer article 16.3

11. What do you understand by growth hormones ? Discuss briefly the recent work in this direction.

Refer introductory part of Chapter 16 and article 16.1

12. Write an essay on "phytohormones".

Refer introductory part of Chapter 16 and article 16.1

13. Write a detail account of the role of hormones in agriculture.

Refer article 16.4

14. What are synthetic hormones ? Discuss critically the role of synthetic hormones in (i) weed control (ii) parthenocarpic development of fruits (iii) pre-harvest drop of fruits and (iv) fruit growth and maturation.

Refer the topic *synthetic auxins* in article 16.1B

For weed control refer article 16.4A(iv)

For parthenocarpic development of fruits refer article 16.4B(ii)

For pre-harvest drop of fruit refer article 16.4B(iii)

For fruit growth and maturation refer article 16.4B(v)

15. Give an account of the non-indole auxins found in plants.

Refer articles 16.2 and 16.3

16. What are natural auxins ? Give an account of the occurrence of any one of them and its role in the plant.

Refer article 16.1

17. Enumerate the plant growth substances and give a brief account of their physiological effect.

Refer *role of auxins* in article 16.1, *role of gibberellins* in article 16.2 and *cytokinins* in article 16.3

Germination and Dormancy

The *reassumption of growth by the embryo in a seed into a new and independent plant* is the main aspect of **germination**. Germination is the beginning of growth and development of the dormant embryo (i.e. showing no sign of life) within the seed, which consists of various changes till its final development into seedling.

This kind of growth and development proceed uninterruptedly from the germination of the seed to its complete maturity. But in a number of plants they experience a suspended growth. *This temporary suspension of growth or inactivity of plant tissues or organs even when conditions are suitable for their germination* is known as **dormancy**.

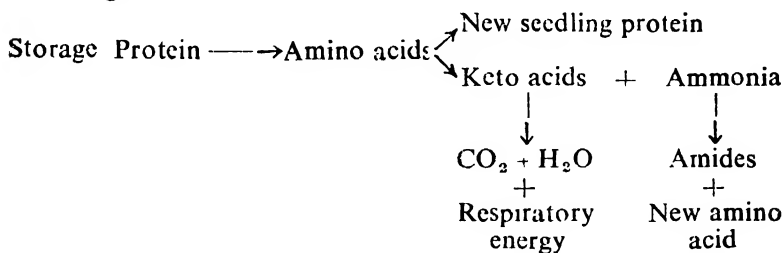
17.1 Physiological processes involved in germination—The initial stage of seed germination is the rapid uptake of water leading to a swelling of the seed tissues. This swelling of the tissues causes rupture of the seed coat (in some cases, however, this does not take place until the emergence of the primary root). Now as the hydration of the cells increases, osmotic forces come into play and control the water uptake by the seeds. The increase of hydration is associated first with the increase in the metabolic activity i.e., in the enhanced respiratory rate within the embryo. The increased respiration in the early stage of germination is not due to availability of respiratory substrate but due to the activation of the enzymes present in it. The small amount of respiratory substrate present in the seed which causes the rise in the respiratory rate is sucrose. The majority of the reserve foods stored in the cotyledons or endosperm are mainly in the insoluble form as polysaccharides (particularly starch), as fats or protein. The rate of growth will depend on the utilization of these insoluble stored food stuffs into soluble forms and their transport to the region of cell expansion and cell division in the embryo. This conversion of insoluble food stuffs into soluble forms is purely an enzymatic process. Some of the enzymes (i.e. respiratory enzymes) are, however, activated in the early stage of water uptake by imbibition whereas the majority of the enzymes involved in the process of reserve food breakdown are synthesized during the germination process. It has been shown by Bakke and Noecker (1933) in *Avena sativa*, that the embryo promotes enzyme formation in the endosperm.

The germination of the embryo is dependant on the utilization of its own reserve food after its breakdown into simpler form by the enzymatic activity in the storage tissues of the seeds. The embryo of the

seeds not only regulates the formation of enzymes but it also directs the flow of soluble substances from its storage tissues to the growing regions. The movement of these substances to the embryo is, therefore, movement from a region of higher concentration to a region where they are rapidly consumed in embryo metabolism. This movement does not however, specify the nature of the actual substances mobilised to the embryo or the mechanism of the translocation process.

In germination, the reserve foods like starch and fats are mainly converted to disaccharides like sucrose, as it is in this form that is transported in the phloem of the conducting strands. α -Amylase and β -amylase are mainly responsible for the conversion of starch to disaccharide units (like maltose), whereas the fats are converted to fatty acids by *lipase* enzymes and ultimately converted to sugar. Since the breakdown products of starch and fats are the main respiratory substrate they are directly consumed in the respiratory process. But the proteins are not utilized in the respiratory process as they are acted on by the proteolytic enzymes to yield equivalent amount of amino acid, simple peptides etc. Proteins are mainly consumed in the synthesis of other organic nitrogenous compounds of the growing embryo.

The breakdown of the seed proteins takes place according to the following scheme :



Although it has been assumed that proteolytic enzymes in the seeds are responsible for such a breakdown but this is not an unequivocal evidence.

The growing embryo also requires phosphorus compounds, vitamins, hormones etc. all of which are found to be released from the storage cells early in the germination process.

Although the exact mechanism of organic solute transport has not been satisfactorily worked out, the soluble food material must pass from cell to cell within the storage tissues, conducted through the vascular strands and then pass out from the strands to the dividing, expanding and differentiating cells of the growing regions. Entry of food materials to the strands adjacent to the growing tissue and their removal in the region of active growth is mainly related with energy derived from the respiration of living cells (i.e. 'active' transport).

The growth of the organ which commences with increase of water uptake, is reinforced by the formation of new cells at the apical point

of the root and in the growing region of the embryo shoot. This process of cell division and cell enlargement is mainly dependant upon release of energy and of some essential reacting molecules from the complex food stuffs.

In the whole process of growth and germination, therefore, the energy and these reactive molecules are essential in the synthesis of a number of new cell materials particularly of the protein and lipid for protoplast structure and of the polysaccharides and polyuronic acid molecule of the cell wall. By the absorption of water the embryo cells are therefore connected with a number of interconnected chemical reactions; some are related with the degradation of the complex food stuff (i.e. *catabolism*) and other sequences result in the synthesis of some unique molecules from which living structures are formed (i.e. *anabolism*).

17.2 Conditions necessary for germination—Refer *Studies in Botany* vol. I., in article *germination of seeds*.

17.3 Dormancy—A large number of ripe seeds and buds fail to germinate until after the lapse of particular period of time inspite (irrespective) of their all favourable environmental conditions. This temporary suspension of growth is definitely due to some internal conditions within the seeds or buds themselves. *This state of inhibited growth of a perfectly viable seed or bud placed in a perfectly favourable conditions for germination is called dormancy.*

Dormancy occurs in a number of plant organs such as seeds, buds, tubers, bulbs and even in roots. Although dormancy has got a 'definite survival value' for wild plants, in cultivated species it does not 'provide any apparent benefit'. Still it is of frequent occurrence among plants. The most important impression regarding the dormancy is that it has got a 'positive value to the plant'.

Dormancy is always associated with the senescence of the entire plant body or part of it. Thus in case of seed dormancy the entire plant is in a state of senescence, while bud dormancy occurs when the leaves are senescing and falling. Like seeds, the dormancy in tubers and bulbs develop when the entire plant is in a state of senescence.

A. CAUSES OF DORMANCY—The seed dormancy in plants may be due to one or a combination of several factors. The two important physiological control of dormancy are (i) those involving structural limitations and (ii) those involving growth substances in the seed. Since the two are not separable, the following catagories will be helpful in discussing the subject.

(i) *Impermeability of seed coat to water*—At maturity a large number of legumes (e.g., alfalfa, clovers etc.) and aquatic plants (e.g., water lotus) develop seed with hard thick seed coats which are completely impermeable to water. Germination cannot take place until water penetrates through the seed coat. This limitation of water by these hard seeds is influenced by the hygroscopically activated valve in the hilum (Hyde, 1954). According to him the failure of

germination even under moist condition is due to limitation of moisture entry due to closure of hilum. Opening and closing of the hilum aperture is due to differential moisture content of internal and external seed coat layers. When there is more moisture in the outside of the seed coat the valve closes and so no entry of water takes place, if, however, there is less moisture in the outside layer, the valve opens and the seed dries further. Hyde thus showed that lower the moisture level of the seed, the greater is the impermeability of the seed coat and thus there is a pronounced dormancy.

Another probable explanation regarding the impermeability of the seed to water is the structure or the chemical composition of the seed coat.

(ii) *Mechanically resistant seed coat*—In a number of plants the seed coats are made with some stony shells which are critical in mechanically limiting the enlargement of the embryo. Seeds of a number of plants e.g., water plantain (*Alisma plantago*), shepherd's purse (*Capsella* sp.), mustard (*Brassica* sp.), etc., retain a considerable period of dormancy as their coats are strong enough to prevent any expansion of the embryo. The failure of the seed coat to burst under this pressure is the main cause of dormancy.

In pigweed high temperature (above 40°C) makes the seed coats less resistant and thus inducing germination. The embryos of this seed have got no dormant period and therefore can grow rapidly when the coats are removed. Any treatment which can decrease the resistant power of the seed coat can increase the percentage of germination.

(iii) *Seed coat impermeable to oxygen*—The seeds of a number of grasses and of many plants of Compositae family have their seed coat considerably limit the exchange of gases in and out of the seed. This causes a pronounced dormancy.

The best example of this kind of dormancy can be exhibited by the seeds of cocklebur (*Xanthium* sp.). Each fruit of cocklebur contains two seeds, out of which the lower seed germinates in the spring if other conditions are favourable, while the upper one fails to germinate under that condition. The dormancy of the upper seed is due to its structural peculiarities which hinder the entry of oxygen. The normal germination of the seed can, however, be restored by rupturing the seed coat or by increasing the oxygen pressure around the seed (Shull, 1911). Under natural condition the seed coat of the seeds gradually becomes more permeable to oxygen due to dry storage which diminishes the intensity of dormant condition.

(iv) *Growth inhibitors*—In some cases chemical compounds are produced in plants which can check the germination of the seeds considerably. These are called *inhibitors*. The inhibitor not only limits growth but also it provides more complex biochemical systems related to the photosensitivity of seeds. The inhibitors are of abundant occurrence in dormant seeds.

One of the dramatic evidences of growth inhibitors can be exhibited by the application of tomato juice to other seeds as well as to tomato seeds. Majority of the seeds fail to germinate by the application of juice. Even in the dilution of 1 : 25 the tomato juice inhibits the germination of seeds of *Lepidium sativum*. This type of wide spread occurrence of growth inhibitor in seeds and in ripening fruits has been shown by Evenari (1949).

Several other chemical compounds have got the property of inhibiting seed germination of which the most important are coumarin (Nutile, 1945) and naringenin (Phillips, 1961). Both of them can inhibit the germination of lettuce seeds. Some of the polypeptides (Elliott and Leopold, 1952) and ferric chloride (Paech, 1953) may also be involved in the inhibition of seed germination.

(vi) *Rudiment embryos*—In the development of the embryo of *Ginkgo biloba*, it has been shown that the embryo does not develop as rapidly as surrounding tissues. So when then seeds of the plants mature the embryos are still in an imperfectly developed stage. Germination of such seeds is naturally delayed till the embryo is completely developed. The other examples of such dormancy of seeds due to incompletely developed embryos include *Ilex opaca*, *Faxinus excelsior* and many orchids.

(vii) *Dormant embryos*—Many mature seeds fail to germinate even when the embryos are completely developed and all the environmental factors are favorable. This condition has got nothing to do with the seed coat, as no germination can be restored by the rupture of the seed coat. Dormancy of this type of seeds is purely due to some physiological conditions of the embryo. The seeds of apple, peach, iris, dogwood, hemlock, pines etc. can germinate only after a considerable period of rest (known as *after ripening*) during which period some physiological changes occur in the embryo. These physiological changes convert a dormant embryo into one that can resume growth. The exact nature of these changes is not clearly known.

B. METHODS OF BREAKING DORMANCY—The seed dormancy presents a special problem of considerable economic importance. Plant growers are often interested to obtain seeds that will have very short dormant period or have no dormant period at all. Majority of the plants have got a considerable dormant period. So methods have been devised to break this dormancy of seeds.

The whole treatment of breaking seed dormancy can be separated into four categories : mechanical (or scarification), temperature (or stratification), light and chemical.

(i) *Mechanical or scarification*—Considerable attention has been paid to the effectiveness of the mechanical removal or *scarification* of the seed coat in breaking seed dormancy. This method can be successfully applied in obtaining germination of seeds where coats are considerably hard or with coats which can limit the entry of gases

or when it is limited by growth inhibitors in the seed coat. Any treatment, be it mechanical or otherwise—which can permit germination should be included within it. The scarification creates a crack on the seed coat which favours the entry of water and thus permit quick germination.

(ii) *Temperature* :

(a) *Low temperature*—Low temperature treatment in breaking dormancy has been known and utilized for centuries. In some cases, very low temperature (near freezing) for a brief exposure, is very effective in breaking dormancy of the seeds; while in others an extended period of exposure is needed. Temperature near freezing ($\pm 5^{\circ}\text{C}$) is usually most effective, though, in some cases 10°C is low enough for the purpose (Crocker and Barton, 1957). This practice of chilling seeds and buds in breaking their dormancy has sometime been given an inappropriate name *seed stratification*.

Low temperature treatment which usually causes an extensive changes in the distribution of food materials from the endosperm to the embryo has been shown by Stokes (1952) in *Heracleum* seeds. Fine and Barton (1958) have shown that in peony seeds accumulation of amino acids takes place from the endosperm to the embryo during cold stratification. Cold treatment can break dormancy of cherry seeds through an unblocking of phosphorus metabolism in the embryo (Olney and Pollock, 1960).

(b) *Alternating temperatures*—Morinaga (1926) first observed a variation in the low temperature treatment and a requirement of alternating temperature in breaking dormancy. Crocker and Barton (1957) have observed increased percentage of germination with alternating high and low temperatures than any single temperature treatment. Toole, *et al* (1955) have shown that by alternating temperatures between 15°C and 25°C the percentage of germination is considerably increased.

Although the effect of alternating temperature in increasing seed germination is not clearly understood, Cohen (1958) has however, shown that the elevation of temperature can bring about a structural change which is promotive of germination. Earlier Brown (1940) had however, shown that elevation of temperature can increase the permeability of gaseous.

This type of treatment is used mainly where the dormancy is inherent in the embryo of the seeds.

(iii) *Light*—Light can be considered as another factor for stimulating germination. Its effect is quantitative, germination percentage being increased with gradual light exposure (Toole *et al*, 1955). Their effect mainly shows an interrelation between light and temperature.

In lettuce seeds, Flint and McAlister (1937) have shown that the red light was the most effective in breaking dormancy whereas the blue or far red light was very inhibitory for germination.

Some seeds have a photoperiod requirement for germination (Block and Wareing, 1954). Thus the seeds of *Eragrostis ferruginea* have a long day requirement whereas the seeds of *Veronica persica* have short day requirements.

Thus light has got a diversity of effects germination. Some seeds are insensitive, others are promoted or inhibited by it (depending on the wavelength requirement for light) and still others are photoperiod requiring.

(iv) *Exposures to high oxygen concentration*—Dormancy of seeds can be effectively broken by exposure of seeds to elevated concentration of oxygen. Exposure of seeds to high oxygen concentration usually decreases the accumulation of inhibitors in the seed coat and thus help in breaking dormancy of *Xanthium* seeds (Wareing and Foda, 1957). Oxygen is mainly involved in the oxidative destruction of the inhibitors.

(v) *Growth regulators and chemicals*—A number of growth regulators like gibberellins, cytokinins have been found to increase germination of seeds by breaking dormancy. Besides growth regulators, a number of chemicals can effectively break dormancy of which the most important is ethylene. Thiocourea and potassium nitrate are also equally effective and they can increase the effectiveness of many dormancy breaking treatments.

SELECTED QUESTIONS

1. Define germination. Describe the physiological processes involved in germination.

Refer introduction of Chapter 17 and article 17.1

2. What do you mean by germination. Enumerate the conditions necessary for germination.

Refer introduction of Chapter 17 and article 17.2

3. Define dormancy. What are the possible causes which lead to the development of dormancy.

Refer article 17.3 and 17.3A

4. Discuss in some details the specific factors involved in the dormancy of seeds.

Refer article 17.3A

5. Write an essay on the methods of breaking dormancy of seeds and buds.

Refer article 17.3B

6. Give an account of the effects of environmental conditions on dormancy of seeds. What physiological changes are noticed in seed beginning to germinate.

Refer article 17.3B (ii), (iii) and (iv) and for the last part refer article 17.1

7. What is meant by dormancy of seeds? Describe the physiological process involved in the germination of seed.

Write in short from the article 17.3. For the last part add article 17.1.

18.1 Definition—Growth is one of the most important and natural phenomena characteristic of living organisms. Plants continuously increase in size and development of new organs takes place throughout their life-cycle. This increase in size is not the ultimate change involved in growth. Thus when a grain of corn under optimum conditions becomes a tall plant, it is a case of increase in size. Another example of increase in size can be seen when a piece of dry wood is dipped into water. In both these cases the cells are stretched as a result of turgor pressure. The difference between these two examples is that in the former the increase is irreversible whereas in case of a piece of wood this increase can be reversed resulting in the decrease in the size of the cells. *Growth therefore is a permanent irreversible increase in size or volume or mass accompanied by an increase in the dry weight.* Growth is the outcome of the complex interplay of a number of metabolic and biophysical processes in the meristematic zones, where the cells divide, enlarge and differentiate. Different authors, therefore, define growth from different angles. Blackman considers growth as a finished products of the metabolic loom where anabolism is more than catabolism. Miller (1954) regarded it as 'a permanent increase in weight attended by a permanent change in form'. Thimann (1960) puts it as 'an irreversible increase in volume'. Bloch in 1961 describes growth as a highly complex process involving more than one master reactions.

Growth therefore involves a variety of diverse and complex phenomena. Growth has been taken as an increase in bulk as a result of division and elongation of cells. It is sometimes confused with the development of plant parts.

Development is considered to be an integrated complex of activities and has got gross phases, (i) increase in volume and (ii) differentiation of specific elements and structures. Growth on the other hand is a process of cell division and enlargement accompanied by an increase in weight and differentiation of structures (due to irreversible changes in the protoplasm and wall of the cells). Growth largely depends on the stage of development of organs, but it occurs in a more systematic manner than random. Growth of the plant can be measured whereas the development can be assumed by qualitative observations. It may be concluded that a plant develops as it grows.

18.2 Site of growth—Growth of the plant does not occur indiscriminately in all regions but only in the region of growing points i.e., in the *meristematic regions*. Meristems are situated in the apex

of the roots and shoots and also in the cambium. The former type is known as *terminal* or *apical meristem* and the latter is known as *lateral meristem*. Growth initiated in the apical meristem of root and stem is called *primary growth*. In many species primary tissues constitute the entire plant while in others the plants increase in diameter as a result of the activity of the lateral meristem. Lateral meristems give rise to secondary tissues which are also responsible for the secondary growth of the plant.

18.3 Phases of growth—The ultimate manifestation of cell division, cell elongation and cell enlargement in a meristematic base is the growth of the plants. The apex of the root and stem can be clearly distinguished into three regions ;

(i) *The phase of cell formation* or *embryonic phase*, it is one of the most important stages of growth, where non-vacuolated cells become mature and multiply.

(ii) *The phase of cell enlargement*—The above cells then become mature. Vacuoles containing cell sap begin to appear and gradually expand. Consequently the cells become osmotically active and fully turgid and thereby increase in size.

(iii) *The phase of cell maturation*—Here the cells elongate to maximum capacity. The cells then gradually become specialized and attain maturity. Characteristic wall thickenings appear in the cells of several tissues. Once differentiated, these remain unchanged so long as they exist.

18.4 Growth patterns—The rate of growth of plant parts is not uniform throughout, even when the external conditions are constant. Growth starts at a very slow rate during the phase of cell formation, the rate gradually increases attaining maximum during the phase of elongation and then gradually slows down in the phase of maturation after which the growth finally stops. This active growth stage during

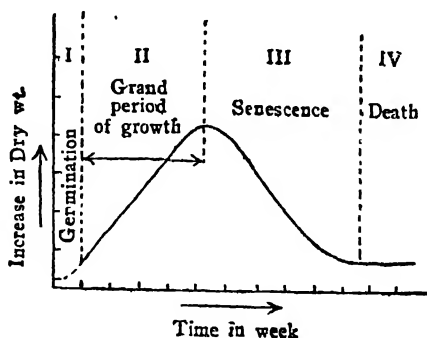


Fig. 18.1 Generalized form of growth curve showing changes in dry weight during growth, senescence and death.

which regular changes in the rate of growth take place is known as *grand period of growth* (Sachs, 1873).

In the growth curve (Fig. 18.1) the initial loss of dry weight is due to utilization of the carbohydrate or fat reserve in respiration during germination (Fig. 18.1[I]). In the next phase of growth (II) there is an increase in dry weight due to accumulation of food materials during photosynthesis and also due to mineral salt absorption. The third stage (III) is the active growth stage represented by the grand period of growth and here there is a loss in dry weight because the rate of respiration is greater than the rate of photosynthesis. In the fourth stage of the growth curve (IV) there is no longer any change in dry weight.

Any change in environmental condition may increase the size of the curve but the general pattern of the curve remains unaffected. This type of growth curve will be exhibited by all plants and also of all types of growth, whether it is measured in terms of leaf area, stem length, volume or weight. If such growth result is expressed in

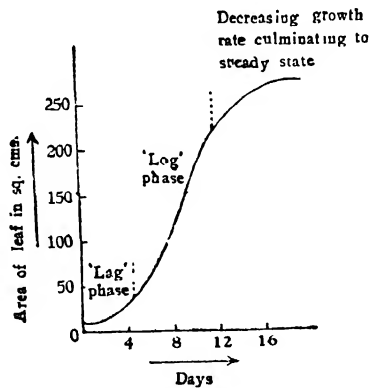


Fig. 18.2 Sigmoid growth curve is characteristic of single cells, tissues, organs, organisms and populations.

relation to time it will produce a typical S-shaped or sigmoid growth curve (Fig. 18.2) which shows that all life is characterised by three distinct stages of growth ; (i) the initial slow rate of growth known as *lag period* ; (ii) followed by rapid elongation and if the logarithm of growth rate is plotted against time it will show a straight line. This phase is known as *log period* of growth and (iii) a phase of slow growth rate which ultimately ceases at maturity. If the curve is further prolonged, a time will be reached when senescence and death of the organism will take place.

The main explanation of this type of curve suggests that hormone activity is one of the essential factors in controlling growth. Hormone inactivation or inhibition causes a variation in the rate of

growth. This pattern of growth may also be due to nutrition basis. Thus in the initial stage the utilization of reserve food starts slowly, which rapidly increases bringing about an increase in growth. This increase continues when the plant develops its photosynthetic mechanism. In the later stage of sexual maturity the photosynthate is diverted to the flowers, fruits and even to seeds. The flow to the vegetative region is cut off and the growth finally stops.

18.5 Factors affecting growth—Regardless of their habitat in which they are growing, plant growth is controlled by the interaction of genetic and environmental factors. Growth usually involves most of the bioprocesses occurring within the living cells and is mainly regulated by the growth substances (i. e., hormones). The basic pattern of growth is determined by the heredity of the plant and the detailed expression of that growth is influenced by a number of environmental factors like temperature, light, oxygen concentration, carbon dioxide concentration, wounding etc. Some of these factors are external, others internal.

EXTERNAL FACTORS :

(i) *Temperature*—It is one of the most important external environmental factor which influence the rate of growth. Most of the metabolic activity ceases below 0°C or above 40°C and since growth involves a series of chemical reactions its activity also ranges at a temperature between 0°C and 35°C .

The velocity of the growth reaction is related to temperature according to van't Hoff's law which means that with a rise of every 10°C there is a doubling of the speed of reaction i.e. Q_{10} (temperature coefficient) is strictly 2 upto 35°C . Above 35°C van't Hoff's law is not applicable as at a higher temperature enzyme inactivation takes place at a rapid rate than at lower temperature.

Like all physiological processes there are three cardinal temperatures for growth—*minimum*, *optimum* and *maximum*. The cardinal points vary considerably with different species, different climates and also for different parts of the same individual and for different stage of development.

The optimum temperature for growth in majority of the tropical and sub-tropical species is found to be 30°C — 32°C . At higher temperature growth depends upon the length of time during which a growing region is subjected to that particular temperature. This is known as the *time factor*. Thus at a lower range of temperature (i.e., upto 30°C) the plant organ may attain a high rate of growth (according to van't Hoff's law) and which may continue for a long period. But at higher temperature (35°C) a maximum rate of growth may be attained but which decreases with time.

If the plant organ is subjected to a drastic change of temperature (from higher to lower or *vice versa*) there is an initial increase in the

rate of growth followed by decrease. This type of reaction is known as *thermo-growth reaction*.

(ii) *Light*—Like temperature it is also an essential factor for growth and it has three cardinal points e.g., minimum, optimum and maximum. It is usually seen that plants grown in shade have larger internodes, poor leaf development, etiolation etc. Whereas plants exposed to normal illumination are healthy with normal growth. As light is directly responsible for photosynthesis, it is expected that it has an influence on growth. In total darkness plants get etiolated and ultimately die.

The effect of light on growth is dependant on (a) intensity of light (b) quality of light (c) duration and (d) direction of light.

(a) *Intensity of light*—Intensity of light has pronounced effect on growth. Normally maximum growth (both as regards increase in length as well as in leaf area) takes place under light intensity much less than that available in the full summer day.

High light intensity usually results in stunted growth due to increase in the transpiration rate. High rate of transpiration leads to a deficiency of water causing retardation in cell division and cell enlargement.

(b) *Quality of light*—The quality of light does not play any important role in the rate of growth, as in nature the quality shows little variation. Light of different wavelengths has different effects. The most effective light as regards growth of the plant is the visible light as compared to any of its spectral zone (Klebs, 1913). In blue light, only the cell division takes place while cell enlargement is retarded. Red light on the other hand influences cell enlargement but inhibits cell division. Leaf blade expands more in green than in other lights.

(c) *Duration of light*—Seasonal variation in the length of daily light period occurs in most parts of the world. This variation in the daily length of the light period has a marked effect on growth and development of plants specially upon the reproductive phase (photoperiodism). Flowering is favoured in a number of plants by short day (where duration of light period is less) while others by long day (where duration of light period is more.)

(d) *Direction of light*—It plays an important role because different plant organs like roots, shoots and leaves have different orientation to the direction of incident light. According to Priestly, the distribution of growth activators (i.e., hormones) varies considerably with the direction of light (cf. *tropic curvatures* article 19.2) and consequently the growth pattern also varies.

When a plant is suddenly transferred from darkness to a very high light intensity there is a marked decrease in the rate of growth which, however, is subsequently recovered and the original rate is attained. This type of reaction under normal temperature and pressure is known as *light-growth reaction*. If, however, on the other

hand, the increase of light intensity is gradual there is a gradual increase of growth rate. The increase in the rate of growth due to high temperature treatment is said to be due to some "shock" produced by the sudden variation of illumination.

(iii) *Oxygen concentration*—Supply of oxygen is necessary for growth, as no aerobic respiration and other metabolic activities can take place without external supply of oxygen. Growing organs require more energy for cell division and elongation and so they respire vigorously. Without oxygen therefore, no growth is possible.

In some cases high oxygen concentration of the air may retard growth.

(iv) *Carbon dioxide concentration*—The effect of carbon dioxide concentration for growth is chiefly through photosynthesis, in supplying food materials for growing cells. Its effect on growth therefore, like photosynthesis is directly proportional with the concentration, provided other factors are not limiting. Higher concentration has however a toxic effect and so growth rate is retarded.

(v) *Wounding*—As a result of wounding, the rate of growth of cells in the region of wounds is increased. The increase in growth is due to some growth promoting substances i.e., hormones (refer article 16.4A [iii]).

(vi) *Water supply*—Growth rate is mainly dependant on the water relations of the growing organs. Cell elongation is dependant upon the capacity for the absorption of water. According to Sachs the enlargement phase of growth is dependant on the turgid condition of the cells and this turgidity is possible through the absorption of water.

INTERNAL FACTORS :

(i) *Hormones*—refer article 16.1G (a).

(ii) *Enzymes*—Various kinds of enzymes (e.g. respiring enzymes) are required for healthy growth of plants as they are concerned with the metabolic activities of plants. The action of hormones (auxin) causes an increased accumulation of enzymes which may be related to growth.

(iii) *Nutrition*—Nutrition and healthy condition of plants play an important role in growth ; with the increase in nutrition such as imparted by manuring, growth increases and is vigorous. When the nutrient is sufficient, auxin is produced more at the tip. In accordance with the availability of the auxins and nutrients the shoot enlarges.

18.6 Endogenous Rhythms of Plants—Many aspects of the metabolism, growth, behaviour and development of plants occur in rhythmic cycles or sequences, generally over a period of a day (24 hours). Although these rhythms are attuned to rhythmic environmental changes such as daily changes in temperature and light

or a seasonal changes in temperature or day length, this rhythmic changes generally continue even when plants are placed in an uniform environment with no fluctuation in any one of the environmental factors. These rhythms are known as *endogenous rhythms* or sometimes as the *biological clock*.

The existence of persistent rhythms in plants was first observed by Bünning. He observed a diurnal movement of leaves in the runner bean (*Phaseolus multiflorus*) in which the primary leaves rise during the early part and later fall towards the evening. This daily rhythms are often referred to as *circadian rhythm*. This rhythmic response may become synchronized or set to the natural fluctuation of some environmental factors. Other circadian rhythms of plants include the daily opening and closing of flowers, the daily changes in the rates of respiration and cell division and perhaps some of the daily growth periodicity.

One example of a plant attuned to a lunar tidal period is the brown alga *Dictyota*, which produces eggs and sperm at about monthly intervals. Among plants, such lunar rhythms are restricted principally to marine algae.

Many of the seasonal or annual rhythms such as the time of blooming, the onset of dormancy, the breaking of dormancy and seasonal growth periodicity are not endogenous since they can be controlled by suitable experimental alteration of the effective environmental factor. Thus a short-day plant (SDP) can be made to bloom earlier by placing it under artificially shortened day indicate that there is probably an endogenous rhythm involved in the photo-periodic responses of plants.

On the basis of this Bünning postulated that there is an endogenous rhythm in photoperiodic sensitivity.

Biologists investigating these rhythms are of two schools of thought. Some biologists think that the rhythm is not truly endogenous and they are really result from rhythmic changes in environmental factors like atmospheric pressure, magnetic fields or cosmic radiation. However, others think the rhythms are truly endogenous and not brought about by any environmental factor, although they may be synchronized with such a factor.

18.7 Measurement of growth—Growth can be measured in terms of increase in diameter of the stem, increase in the area of the leaves, increase in the volume and increase in the dry weight or fresh weight of the materials.

Of all the indices for growth, measurement of the linear growth of the stem has a considerable practical value for such purposes.

A. MEASUREMENT OF LINEAR GROWTH—The rate of growth in length can be measured in the following ways :

(i) *By direct method*—The rate of growth in length can be measured at intervals simply by means of an ordinary scale and to find the increase in length during the period.

It is a very crude method of measuring growth rate and can be effective only over long intervals of time.

STUDIES IN BOTANY

- (ii) By an arc indicator or auxanometer—An arc indicator consists of a graduated steel quadrant. This quadrant is fitted with a wheel placed at the centre of the circle. A long pointer is fixed with the wheel, the free end of which moves upwards and downwards upon the graduated arc.

To determine the growth of a plant, the apex of the stem is attached with a string which is then passed over the wheel, the other end of the string is attached with a small weight, in order to keep it stretched (Fig. 18.3). Now the position of the pointer of the arc is noted. Whenever the stem elongates the wheel rotates and the pointer on the arc moves.

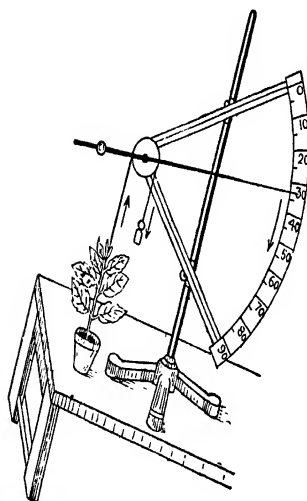


Fig. 18.3 An arc indicator.

- The difference in the position of the pointer before the experiment and after the deflection indicates the amount of growth of the stem in a magnified way.
- (iii) By automatic auxanometer or auxograph—It has been devised by Pfeffer. The main principle of this instrument is to automatically record growth rate both during day and night on the surface of a revolving smoked drum.

It consists of a small wheel over which passes a thread. One end of this thread is attached to the apex of a growing stem. The thread is kept stretched by a counter-balancing weight kept on the other end of the thread. Pass another thread over the larger wheel on which the smaller wheel is fixed. A pointer is now attached to stretched by placing two small and equal weights. This thread is now attached to its one end and is allowed to touch on a smoked surface of a paper, fastened round a cylindrical drum. The drum is now rotated slowly upon its axis. As the stem grows in length, the smaller wheel rotates and also the larger one (as it is fixed on one another). So the pointer also moves accordingly in a highly magnified way and traces markings on the smoked surface of the paper.

From the rate at which the drum rotates, the rate of elongation can be easily calculated which indicates the magnified rate of growth. The actual rate can be calculated from the ratio between the radii of the large and small wheel.

B. RATE OF GROWTH IN DIFFERENT REGIONS OF ROOT TIP—Healthy germinated gram seed with straight radicle, about 2.5 cm long, is taken. The radicle is

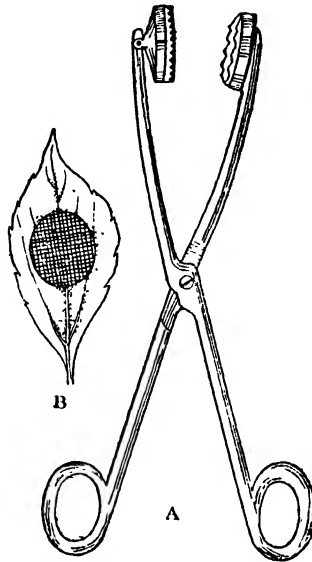


Fig. 18.4 A space-marker disc.

marked at equal intervals with Indian ink by space marker wheel (Fig. 18.4). The seed is now placed under proper condition for germination.

After a few days (preferably two days) it will be found that the distance between the two marks on the radicle just behind the tip is increased considerably, whereas

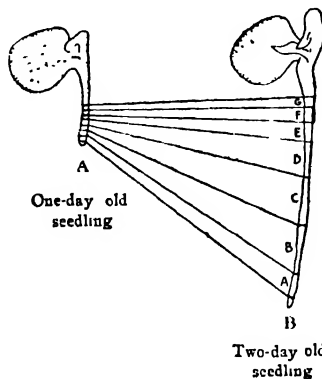


Fig. 18.5 Detection of zones of root tip elongation.

near the base it is not increased. This proves that the maximum growth takes place behind the tip (Fig. 18.5B). This is the region of cell elongation.

SELECTED QUESTIONS

1. Define growth. How can it be distinguished from development ? Describe various types of growth patterns in plants.

Refer articles 18.1 and 18.4

2. Describe the possible environmental factors which affect plant growth. Discuss critically the role of light in this process.

Refer article 18.5

3. Give an account of internal and external factors that affect growth and development in plants.

For the factors of growth refer article 18.5 and for the development refer Chapter 19, article 19.2

4. What do you know by "grand period of growth ?"

Refer article 18.4

5. What do you mean by endogenous rhythms of plants ?

Refer article 18.6

The Physiology of Flowering

“We cannot understand an organism by studying it only on the molecular level” (Went 1962) nor we can study it from the cellular or tissue level. We can study it elaborately by observing the complicated changes in the developmental cycle. This cycle starts with the germination of seeds, gradually attains its juvenile phase and then to maturity followed by a state of senescence. With the onset of maturity the organism changes from vegetative to reproductive phase with the initiation of development of flowers, then to fruits and again to new generation with the development of seeds. Each and every stage requires some physiological actions which give some exciting features of the system. It gives rise ultimately to some information regarding the mechanism controlling the development¹ of plant parts.

19.1 Initiation of flowering—The most fundamental problem of modern biology is the origin of form. While genes control the ultimate form of the living organism, their behaviour in the development of organs is very interesting since certain genes are only active at certain times. Apical cells of the plants are continuously dividing and enlarging to form stems and leaves. At a certain stage, however this tip instead of giving vegetative parts, develops into highly specialized structure, the **flower**. This redirection of growth to the initiation of flowering is due to some chemical substances not synthesized in the apex of the stems, but in the maturing leaves. This chemical substance is of hormone type which is yet uncharacterised and it arises in response to some external environmental change to provoke the *initiation of floral meristem, the development of flowers and anthesis* itself. The manner in which all these changes take place by a flowering hormone, which incidentally also arises in response to the environmental change is an important problem of the physiology of flowering.

The original idea of Klebs (1913) has got immense value in explaining the flowering response of plants due to daylength and temperature. *Photoperiodism* is usually applied to describe the response of plants to daylength and *vernalization* is the response of plants to temperature treatment.

19.2 The environmental factors that cause flowering :

A. Photoperiodism—Length of the day technically known as *photoperiod* is one of the most important factors responsible for

¹ *Development* is the progressive change in the characteristics of the new organs produced by cell division ; *growth* whereas means an increase in size.

growth and development of plants. Garner and Allard (1920) first demonstrated a detailed investigation of facts that might cause certain plants (e.g. tobacco, soyabean) to flower. They attempted to regulate the flowering by varying the temperature, nutrition and soil moisture but none of these factors was found to affect the date of flowering very markedly. Both these species flower when the days are shorter. There are other species (e.g. spinach, henbane) which flower when the days are longer. The flowering can therefore be initiated by exposure to different day lengths. This phenomenon of response of plants to day length is known as photoperiodism.

A great many facts about photoperiodism have accumulated since the formulation of the principle by Garner and Allard in 1920. These facts are not only numerous but complex and it does not appear to be possible to-day to put all of them together into one coherent model.

Biologists are now aware that plants may be classified with respect to their responses to relative length of day and night as *short-day plants* (SDP), *long-day plants* (LDP) and *day-neutral plants*. Day-

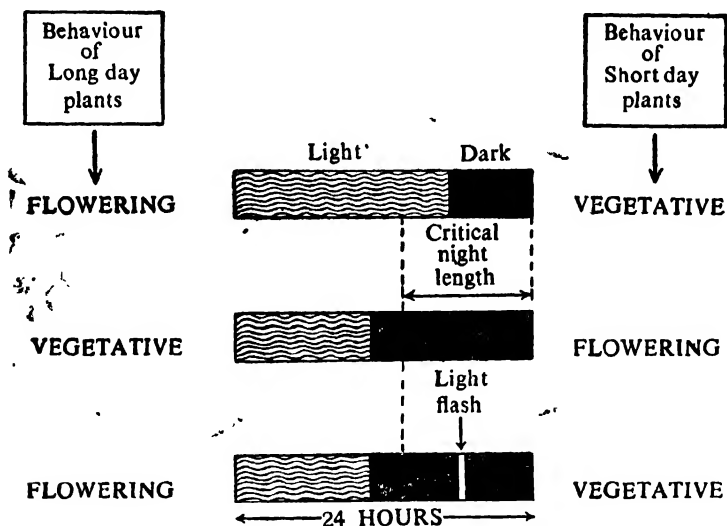


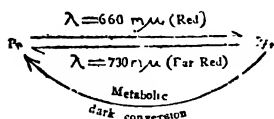
Fig. 19.1 The effect of a light flash interruption of the dark period on flowering in short-day and long-day plants.

neutral plants are those which disregard relative length of day and night and in which flowering is controlled by other factors like age, number of nodes and previous history of cold treatment. The *short-day plants* flower only under day lengths shorter than some critical value. The *long-day plants*, on the contrary, flower only under day lengths longer than a critical value. Actually the two groups might better be referred to as long-night and short-night

plants respectively, since the length of the dark period is the primary determinative factor in each case (Hamner and Bonner, 1938 ; Lang and Melchers, 1943). Common examples of strictly short-day plants are the varieties of tobacco, *Xanthium*, soyabeans, *Pharbitis* and *Poinsettia*. Some common strictly long-day plants include *Hyoscyamus* (henbane), spinach, plantain and winter barley. Tomato, maize and cucumber are the day-neutral plants. Generally speaking SDP flower when exposed to light-dark cycles containing dark periods longer than the critical value. LDP flower only when exposed to light-dark cycles containing dark periods shorter than the critical value. Or, we may define short-day and long-day plants roughly in still another way based upon their responses to interruptions of a long dark period by a light flash. SDP produce flowers when grown on a regime of long nights and this flowering is inhibited by a light flash given during the night (Hamner and Bonner, 1938). LDP, on the contrary, do not flower when grown on a regime of long nights ; but do flower if this long night is interrupted by a light flash (Katunskij, 1936) (Fig. 19.1).

The light interruption phenomenon on the flower initiation, therefore opened up a world of possibilities. First of all to show when this light interruption was most effective and how much light is required to bring about the response.

Secondly, which wavelength of light is most useful. Green colour of the visible spectrum is normally ineffective in inducing flowering, whereas blue spectrum induces poor flowering. It has been found by Hendricks and Borthwick (1952 ; '63) that the most effective region is in the red ($660m\mu$) like all other light-controlled systems. Thus it is implied that the pigment system acting in photoperiodism is the same as that occurring in other photo-responses. Further the effect of red light could be reversed by exposing the seeds to light of longer wave lengths (i.e. in the far-red region, $730m\mu$). Thus the pigment involved in this phenomenon is converted from one form to another and this reversible red \rightleftharpoons far-red photo-reaction exerts a controlling influence on growth of plants. The essential idea of such an investigation has been summarized as below :



The photoperiodic effectiveness of a dark period, may be negated by light even of very low intensities. In other words, definite, alternate periods of light and darkness are required. Many other growth responses, including seed germination are regulated by the same rhythms of day and night (Borthwick *et al*, 1956).

The work of Parker, *et al* (1946 ; '50) clearly showed that plants contain in the dark a pigment which absorbs red light ($660m\mu$)

thereby negating the photoperiodic effectiveness of a long dark period. By absorption of red light the pigment appears to be converted to a

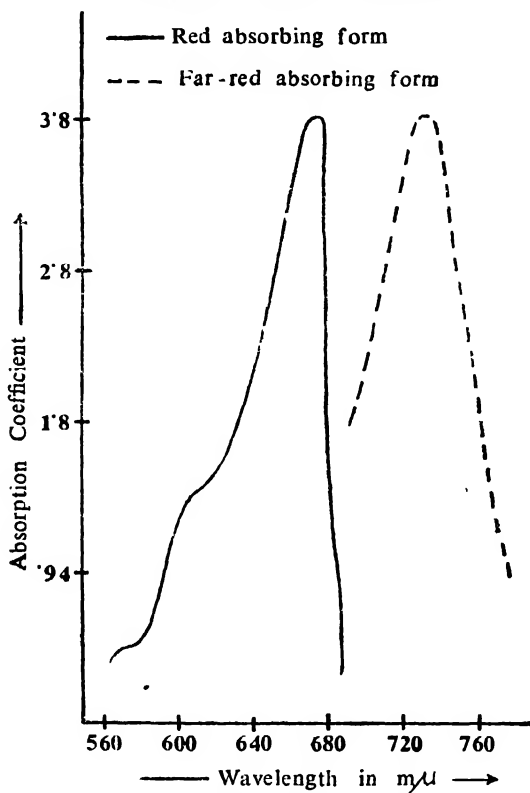
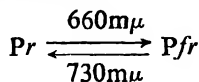


Fig. 19.2 Absorption coefficient of the red and far-red absorbing forms of phytochrome (modified after Hendricks, 1959).

different pigment which absorbs at longer wavelength, with a peak in the near infrared (710mμ and 730mμ). The form of the pigment which absorbs light (660mμ) is designated as *Pr* and the form which absorbs far-red light (730mμ) is termed *Pfr*. These two forms are interconvertible as shown below :



Thus, if a red light treatment is immediately followed by a near infra-red treatment the plant behaves as though it had been maintained in darkness. Photoperiodic behaviour is thus mediated in part by what we refer to as a pigment called *phytochrome* (Butler *et al*, 1959). Chemically, phytochrome is a chromoprotein with a prosthetic group which is probably an open-chain pyrrole. It is

evident that the red/far-red reversible changes involve a shift in the position of two hydrogen atoms, which results in a change in the position of double bonds. Phytochrome has now been extracted from a variety of plant species.

Action spectra evidence indicates that the pigment system for induction has a single maximum at $660\text{m}\mu$ (red) with relatively little absorption in the blue. The only native pigments in the plant kingdom that have been observed to have this particular characteristics are the straight chain tetrapyrroles in which the four pyrrole rings are not closed into a major ring, such as biliverdin and the algal pigment phycocyanin.

The mode of action of phytochrome on flower induction is still not understood, but it would appear that the *Pfr* form is inhibitory to the flowering process in SDP, whereas is LDP *Pfr* promotes the flowering processes.

The flowering stimulus: Since this tetrapyrrolic type of pigment is present in the green parts of the plants, the leaves are the perceptrors of the radiant energy and as it is the bud that flowers in response to photoperiodic treatment of the leaf, it is obvious that there must be some transmission of 'stimulus' between leaf and bud. This stimulus may be either something that promotes flowering and travel from leaf to bud or something that inhibits flowering, which is normally stored in the bud and which is somehow absorbed by the leaf as a result of photoperiodic treatment. In short-day plants, therefore, something that promotes flowering is produced by the leaf as a result of appropriate photoperiodic treatment and then travels from leaf to bud. For this peripatetic stimulus the name '*florigen*' was proposed by Chailachjan in 1936.

The grafting experiments of different workers have revealed that it is the same chemical substance that is produced in all species of plants, although its chemical nature is unknown and all attempts to isolate it have also failed. Lincoln, Mayfield and Cunningham (1961) claimed partial success in determining the chemical nature of this hormone. The active fraction of this extract in acidic and Lincoln (1964) named this active substance as *florigenic acid*. Whatever may be its exact chemical nature, even today we use the term '*florigen*' for this active substance.

The florigen which is produced in LDP as a result of exposure of their leaves to long days, is physiologically identical with the florigen produced by SDP as a result of exposure of their leaves to long nights.

It has been found that synthesis of florigen in leaves is not only dependant on definite light period but also on a definite dark period. Consequently, we should speak of *long-night plants* rather than *short-day plants*. The long-day plants should also be designated as *short-night plants*. But these terminology was changed because of "inertia usual in such matters."

It appears further from the work of a number of workers (Hamner, 1954 ; Salisbury and Bonner, 1955) that the substance that promotes flowering which is produced in one favourable dark period can be accumulated and added to those produced during the next dark period. The effects of successive cycles of photoperiodic treatment are additive. Thus plants treated with a minimum of photoperiodic induction, flower slowly over long periods of time ; whereas the plants treated with a greater number of cycles or with dark periods of greater length, flower rapidly and vigorously over long periods.

So, we can think of photoperiodic induction as a catenary sequence of processes. This catenary sequence consists of several

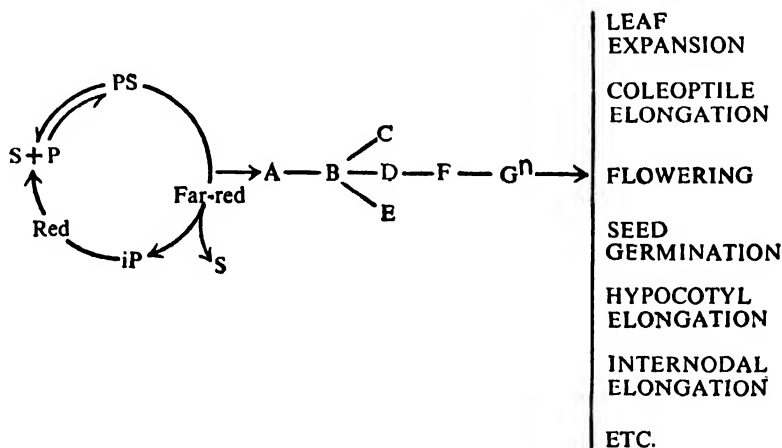


Fig. 19.3 Photoperiodic cycle

individual steps which can be described by the mnemonic HPTHSTI. The letters of this mnemonic stand respectively for ; initial high intensity light reaction (H), pigment decay (P), time measuring (T), hormone synthesis (H), stabilization (S), translocation (T) and induction (I).

The formation of flowering hormone—The whole scheme regarding the synthesis of flowering hormone has been formulated by Gregory

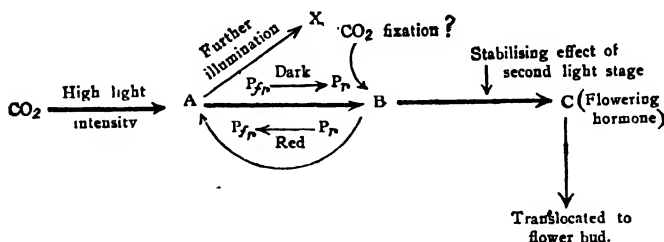


Fig. 19.4 Stages of formation of flowering hormone in SDP.

(1948). He postulated that carbon dioxide in high light intensity is converted in the leaf to a substance 'A' which, however, with further illumination is converted to a leaf forming substance 'X'. In the dark period 'A' is converted to 'B' which is ultimately converted to 'C' i.e., a flowering hormone (Fig. 19.4).

The interruption of dark period depends on the reaction in which $A \rightarrow B$ takes place. If the dark period is interrupted by a flash of light in the beginning there is no inhibiting effect on the synthesis of flowering hormone. Since, still there is enough time for the formation of B from A . If the interruption is near the end, here also there is no inhibiting effect since an adequate amount of B has already been formed. If the interruption of the dark period is midway, sufficient amount of B may not be formed and flowering will, therefore, not occur. A similar case of shortage of B will also result, if the dark period is too short.

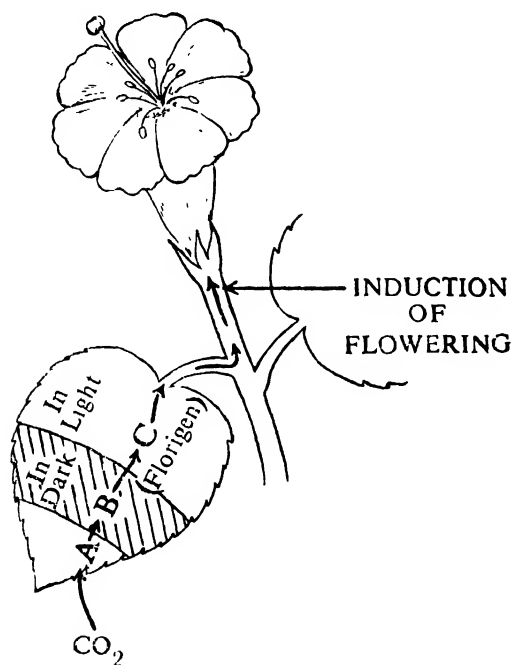


Fig. 19.5 Sequence of events leading to a photoperiodic response.

Thus the whole phenomenon of flower initiation is a florigen initiated process, whereas the development of flower-buds is a growth promoting process dependant on the auxin concentration, water and photosynthate. Thus there must be a close correlation in the auxin-florigen balance. Further, Lang (1957) suggested that the gibberellins

show similar effects to those produced through the phytochrome system and so there must be a correlation also between GA concentration and florigen synthesis. Thus for long-day plants florigen synthesis takes place only at a higher GA concentration whereas short-day plants can synthesize florigen when the concentration of GA is low. Gibberelline-like substances must therefore be included in theories to explain photoperiodic reactions.

Brian (1958) showed that gibberelline-like hormone is produced during light period in the following way.

$\text{CO}_2 \longrightarrow \text{Precursor} \longrightarrow \text{Gibberelline-like hormone}$

In the dark, the decay of the gibberelline-like hormone takes place and which further accelerates in the far-red irradiation. Red irradiation, however, promotes the formation of the gibberelline-like hormone. Further observation on it showed that this gibberelline-like hormone controls the formation of florigen and is responsible for the formation of flowers in both long-day and short-day plants. The complete scheme of flowering can be epitomized as :

$\text{CO}_2 \xrightarrow[\text{Far-red}]{\text{Red}} \text{Precursor} \rightleftharpoons \text{Gibberelline-like hormone} \cdots \rightarrow \text{Florigen}$

TABLE 12
Principal photochemical reactions in higher plants

<i>Photoprocess</i>	<i>Reaction or Response</i>	<i>Products</i>	<i>Photoreceptors</i>	<i>Action spectra peak</i>
Chlorophyll synthesis	Reduction of protochlorophyll	Chlorophyll-a Chlorophyll-b	Protochlorophyll	Blue : 445 m μ Red : 640 m μ
Photosynthesis	Dissociation of H ₂ O into 2[H] and $\frac{1}{2}\text{O}_2$ and reduction of CO ₂	Reductant [H] Phosphorylated compounds.	Chlorophylls Carotenoids	Blue : 435 m μ Red : 675 m μ
Blue reaction	1. Phototropism 2. Protoplasmic viscosity 3. Photoreactivation	Oxidised auxin, auxin system and/or other components of the cell	1. Carotenoids and/or flavin 2. Unknown 3. Pyridine nucleotide, riboflavin etc.	1. Near UV : 370 m μ Blue : 445 m μ 2. Uncertain 3. Uncertain
Red, far-red reaction	1. Seed germination 2. Seedling and vegetative growth 3. Anthocyanin synthesis 4. Chloroplast responses 5. Heterotrophic growth 6. Photoperiodism 7. Chromosome response	Biochemistry completely unknown	Possibly tetrapyrrole	1-6. Induction by red : 660 m μ reversal by far-red : 710 m μ & 730 m μ 7. Far-red induced, red reversal, spectral details uncertain

B. Vernalization—Temperature provides another environmental effect on the seasonal changes of plant body. A large number of plants can be induced or promoted to flower by low temperature (3°C) followed by exposure to long days (i.e. 15 hours) at an optimum temperature.

This promotive effect of low temperature on flowering is termed as vernalization. The term is also applied to the treatment of seeds and other plant organs at relatively high temperature (Sircar, 1948).

The word *vernalization* was first coined by Lysenko (1928) although Klippart and Gassner (1918) had demonstrated the presence of this active principle many years before.

This phenomenon has been demonstrated with cereals, where both the winter and spring varieties are known. Vernalization actually includes the induction of flowering in species which require low temperature (e.g. cabbage, beet etc.) as well as hastening of flowering which is promoted by low temperature (e.g. the winter grains, radish etc.).

In some species, both the seeds and the plant organs are capable of responding to vernalization. Many consider that the rapid growth of the plant may have an antagonistic effect on the flowering response and according to them the low temperature treatment may be simply a suppression of growth (Thompson, 1929 ; Cholodny, 1936). Although many (Gott *et al*, 1955) deny the fact that growth check is the essential part of vernalization, but still the works of Steinberg (1952) and Lewis (1953) strongly support the idea that suppression of growth is specially involved in the response. So this cannot explain wholly the phenomenon of vernalization.

The other possible explanations of vernalization came from the works of Lang and Melchers (1943), who consider that the low temperature may quantitatively displace the critical photoperiod for flowering or low temperature may increase the responsiveness to photoperiod without altering the critical day length needed (Cathey, 1957) or it may completely replace the photoperiodic requirement (Koller and Highkin, 1960).

Sites of vernalization—It has been found by many (Chroboczek, 1934 ; Purvis, 1940 and others) that the apical meristem is in fact the locus of vernalization. Although the work of Wellensik (1961,'62) on *Lunaria* strongly indicated that the leaves could receive the vernalization stimulus only if they experience active cell division. So it may be said that the dividing cells are the sites of vernalization.

Unlike the photoperiodic stimulus the product of vernalization is quite immobile. Thus when the active meristems are vernalized, the inactive meristems are quite non-vernalized.

The vernalization effect is manifested in two morphological changes in the plant organ. One is the extensive development of vascular tissue leading to the growing point and ultimately supplying more translocated substances to the meristems after vernalization

(Chakravarti, 1950 ;'54). Another morphological change involves the enlargement of the embryo at the expense of endosperm, suggesting the mobilization of substances to the meristems (Stokes, 1952).

The result of various workers on grafting experiments clearly indicates the existence of the hormone, **vernalinal** (the name was first proposed by Melchers, 1939) and which is thought to act as a precursor of florigen or as a catalyst for florigen production. Further clarification on the nature of vernalinal came from the work with gibberellic acid. Application of high percentage of gibberellic acid to non-vernalized henbane (*Hyoscyamus niger*) results in the formation of a flowering stem, even under short day conditions (Lang *et al*, 1957) Under long day condition also, the plants will flower, although they sometime contain a higher percentage of aborted seeds.

Although some are tempted to add vernalinal in the list of plant hormones but it must be remembered that very few plants have the ability to transmit the effects of vernalization by grafting

Further, to discuss the site of low temperature effect the work of Cholodny (1936) received special attention. He postulated that by low temperature a special substance (a flowering hormone) is produced in the endosperm of seeds which migrated to the embryo on germination.

Von Denffer (1950), however, is of opinion that the low temperature prevents the formation of an inhibitor of flowering. Under anaerobic conditions this inhibitor is formed even at low temperature and that is why vernalization fails in absence of oxygen.

To sum up, the vernalization effect on flowering is that the dividing cells receive a low temperature stimulus which alters the morphological expression of growth.

Significance of vernalization—It has got an immense role in agriculture. Colder countries like Russia have been successfully applying this process to shorten the vegetative period of plant species and to make them early flowering. The main advantage of this process is that the plant can complete its life cycle (with the formation of flower and seeds) before the onset of the winter season which would normally fail to produce flowers and seeds.

Other advantages of this process are to increase the cold resistance and drought resistance of plants. Sometime disease resistant plants can also be produced by the process of vernalization.

Devernalization—After vernalization, the nullifying effect at high temperature was reported by Thompson (1929), Miller (1929), Chroboczek (1934) and others. Thus the vernalised seeds completely revert to their normal condition if dried at higher temperature for several hours or simply stored under normal condition. *This reversible effect of vernalization by the temperature is known as devernalization.*

Devernalization can be obtained not only by high temperature (35°C) but also can be obtained with anaerobic condition (Gregory

and Purvis, 1937). These findings of different workers clearly signify that an unstable product is formed due to cold treatment which can be metabolized away if high temperature or anaerobiosis is experienced too early to establish its effect.

Devernalization has got an important application in horticulture in the control of flowering of onions and in a number of other plants.

19.3 Effects of gibberellins and other growth hormones on flowering—Although attempts to regulate flowering by the application of auxins have almost all been unsuccessful, the application of gibberellins (GA_3) can induce flowering to a number of LDPs under short day. LDPs which respond to GA_3 form a pronounced rosette under short day and show marked internode elongation ("bolting") under long-day. By applying GA_3 to such a species growing under short day stimulate the internode elongation and this process is accompanied by flower initiation.

The ability of gibberellin application to cause rosette plants to elongate in a manner suggestive of bolting led quickly of the possibility that gibberellins could cause flowering in rosette plants. In fact, it was found to be widely effective. The effects are dramatic and widespread among many species of plants. The stimulation of flowering by gibberellins can be assigned to two groups of plants : those that caused to flower by low temperature and the LDPs.

An extensive array of cold-requiring species is brought to flowering by gibberellins, including the biennial *Hyoscyamus*, the biennial cruciferous plants (e.g. cabbage, beet, turnip) and the cold requiring species (e.g. carrot). Though not all cold requiring species have been induced to flower with gibberellin.

The relation of photoperiod requirements is more complicated. Numerous LDPs have been induced to flower with gibberellins. Among the LDPs gibberellins have been shown to cause or promote flowering in spinach, lettuce, radish, *Hyoscyamus* and others. But in each case, where it is effective, the species is a rosette plant which bolt before flowering. Species which are LDPs but not rosette in form do not flower in response to gibberellins (Lona, 1956 ; Burk and Tso, 1958). If a partial photoperiodic induction is given, many LDPs which were otherwise insensitive will then respond. Gibberellins usually replace long-day requirement of the LD-SDP *Bryophyllum* and will inhibit the flowering of the SDP *Kalanchoe* in a manner suggestive of long-day treated leaves.

Measurements of natural gibberellin content increase after low temperature induction of biennial *Hyoscyamus* (Lang, 1960). Radley (1963) found that in LDP spinach there was a brief detectable rise in extractable gibberellin during the first day of long-day treatment but later on the content decreases. The commencement of bolting therefore might cause a more rapid turnover of the natural gibberellin, accounting for the decline.

It is therefore suggested that gibberellin might be considered a component of the flowering hormone (Cajlachjan, 1958) or better still, a flower promoter through its stimulation of stem growth and perhaps of some mobilization actions associated with growth (Lang, 1957 ; 59).

One reason for the lack of response by some LDP or cold requiring plants might be that the particular gibberellin applied is not effectively used by the plants. Out of 40 gibberellins the effectiveness of 9 gibberellins in stimulating flowering have been described (Wittker and Bukovac, 1962).

In addition to gibberellins, a number of growth regulators both natural and artificial have been found to promote flowering in some species under certain conditions. Thus under certain conditions, kinetin and adenine will promote flowering in *Perilla* and zeatin does so in a aquatic plant (*Wolffia microscopica*). Similarly, the naturally occurring growth inhibitor, abscisic acid (ABA) promote flowering in *Pharbitis*, *Ribes* and *Fagaria*. A number of synthetic growth regulators like CCC, B9, MH, triodobenzoic acid also have been reported to promote flowering in a few species.

In conclusion it can be observed that flowering behaviour cannot accounted for in terms of known growth hormones and yet all attempts to extract a specific flower hormone have been unsuccessful, may indicate that we have adopted an oversimplified approach to the problem, in assuming that flowering is controlled by a single specific hormone. The isolation and identification of the flowering stimulus remains one of the most challenging problems in plant physiology.

SELECTED QUESTIONS

1. Define photoperiodism. Give a detailed account on the transmission of the photoperiodic stimulus.

Refer article 19.2A

2. Describe that the onset of flowering in photoperiodically sensitive plants is due to the production of a specific floral hormone. What do you know about the nature of this hormone ?

Refer article 19.2A

3. Write an essay on the recent developments in the study of photoperiodism.

Refer article 19.2A

4. Write an essay on "hormones and control of flowering".

Refer topic *the formation of flowering* in article 19.2

5. Define vernalization. Give a detailed account on the transmission of the low temperature stimulus.

Refer article 19.2B

6. Give a brief account of the environmental control of flowering.

Refer article 19.2

7. Write an essay on the physiology of flowering.

Refer article 19.2

8. Write a note on phytochrome.

Refer article 19.2

9. State how growth is different from development. Describe briefly the effects of environmental factors on development.

Refer introductory part of Chapter 19. For latter part refer briefly article 19.1, 19.2A and 19.2B

10. Describe the role of gibberellins and other growth hormones on flowering.

Refer article 19.3

Plant Movements

Movements are of universal occurrence in plants although we are often misguided to think of plants as being stationary i.e., without any appreciable sensitivity or movements. This is due to the slowness with which the movements take place.

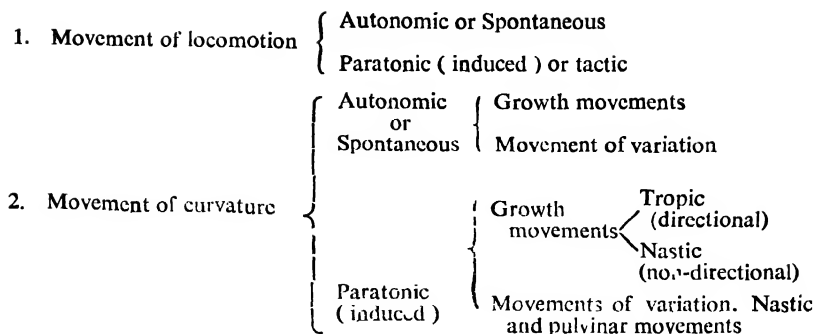
These movements are quite different from the type of movements exhibited by majority of animals and this is probably due to the difference in their modes of nutrition. As the animals have to depend for their nutrition from outside source they must move bodily from one place to another in search of nutrition. So they developed towards mobility and the movements are quite apparent. The plants, on the other hand, as they prepare their food from the raw materials obtained from the environment in which they grow, evolved towards stability. Since majority of the seed plants are fixed in the soil they are not motile like higher animals, but do display their movements by simply bending their parts. Such type of movements is **curvature movements** e.g., the bending of the tentacles of insectivorous plants, twisting elongation of certain plant parts or the opening and closing of flowers. Nevertheless, some unicellular ciliated alga (e.g., *Chlamydomonas*, *Volvox* etc.), many bacteria, the reproductive cells (i.e., zoospores, gametes) of many algae, fungi, bryophytes etc. and the plasmodia of myxomycetes move freely from one place to another. Such movements are called **locomotory movements**.

In general, the plant movements, whether of curvature or locomotory type, are induced by variety of stimuli like temperature, light, gravity, mechanical contact or due to change of turgor pressure in certain cells. The movement induced by a stimulus from within the cell or majority of locomotory movements are *autonomic* or *spontaneous*, whereas the external stimuli produce *paratonic* movements.

Though majority of the plant movements are very slow, but a fairly rapid movement is exhibited by the sensitive plant (*Mimosa pudica*). Here, when the terminal leaflets are touched, all the leaflets at once close down and the leaf as a whole drops down. This movement is due to change in the turgor of the pulvini. Such pulvinar movement is known as **movement variation**.

20.1 Classification of plant movements—Plant movements are broadly classified into two broad classes :

- (i) Movement of locomotion
- (ii) Movement of curvature



20.1 A Movement of locomotion—When the entire organism changes its position freely from one place to another e.g., unicellular ciliated motile algae, bacteria, they are called *locomotory movements*. These may be of the following types.

(i) *Autonomic or spontaneous movements*—These are not governed by any external stimuli but the internal protoplasmic changes of the organism are the main cause of this movement. Thus the ciliary or amoeboid movements of unicellular organism are the example of this type of movement. Rotation or circulation of the protoplasm within living cells is also included within it. Movements of certain moving algae (e.g., *Chlamydomonas*) are noteworthy.

(ii) *Paratonic (induced) or tactic movements*—Here the movements are governed by external stimuli like light, temperature, chemicals etc. and hence are called *tactic movements*.

The tactic movements may be named chemotactic, phototactic, thermotactic etc. depending on whether the inducing stimulus is chemical substances, light, temperature etc. The chemical substances secreted from the archegonial neck helping to move the antherozoids towards it is the best example of chemotactic movement. Bacteria too, move similarly with the supply of free oxygen.

Many algae move towards the shaded bank because of their attraction towards the weak light. Since the movement is governed by light it is known as phototactic.

The best example of thermotactic movement can be seen during the differential rotation movement due to increase of temperature in the leaf of *Vallisneria*.

20.1 B Movements of curvature—Majority of plants do not possess active movements but show movements of their fixed organs simply by changing their position from one direction to another. Such movements fall within the category of *curvature movement*. It can also be grouped into :

(i) *Autonomic or spontaneous movements*—When the movement is induced by internal stimuli it is called *autonomic or spontaneous movement* which include :

(a) *Growth movement*—This type of movement is known as *nutation* and is observed in the twinning plants. It is also found in tendrils, roots, pedicels of flowers etc. Twinning nature of the plant is the result of unequal growth of the stem. As long as the growth continues nutation goes on. According to Darwin the intermode begins nutation slowly, then increases its speed. It is a very common fact that nutation in all members of one particular species takes place in the same direction.

This movement of nutation may take place either in clockwise direction (e.g., *Tamus*, *Humulus* etc.) or anti-clockwise direction (e.g. *Lygodium*, *Phaseolus vulgaris* etc.)

(b) *Movement of variation*—Another kind of autonomic movement is the *movement of variation*, which is caused by the reversible changes in the turgidity of cells. In some cases variation movements are caused by external stimuli like sudden shock, touch, heat etc., when these movements fall under the category of autonomic-paratonic instead of spontaneous.

The best examples of variation movement can be exhibited by the movement of leaflets of telegraph plant (*Desmodium gyrans*). The two small lateral leaflets display such movement. The movement in *Desmodium* leaflets is effected by changes in turgidity of the pulvinus of the leaf stalk.

The variation movement in the leaflets of *Oxalis* is also due to the periodic changes in the turgidity of the cells of the pulvinus.

(ii) *Paratonic or induced movement*—When the movements are induced by the influence of external stimuli, they are termed as *paratonic movement*. It can be grouped into :

(a) *Tropic movements*—When the direction of the response bears a definite relation to the direction of the stimulus (either towards or away from the stimulus) the movement is termed as *tropic movement*. The external stimuli may be light, gravity, moisture or contact and consequently the movements are phototropic, geotropic, hydrotropic or thigmotropic in nature.

(b) *Nastic movements*—The movement in which the response i.e. movement of plant organs, bears no relation to the direction of the stimulus is known as *nastic movement*. According to the nature of the stimuli nastic movements may be photonasty (light), thermonasty (temperature), chemonasty (chemical substances), nyctinasty (both light and temperature), seismonasty (touch, shock etc.).

These movements have got a diversified biological advantage. In the opening and closing of flowers these movements increase the chance of fertilization and are thus concerned with the survival of the race. The movement of leaf due to nastic movement causes reduction in the leaf surface exposed to light thus diminishing transpiration which has a definite advantage during water shortage. The movement exhibited by the insectivorous plants also help in the absorption of nitrogenous food materials.

20.2 Individual tropic movements—All tropic movements (tropism) are paratonic curvature i.e. growth movements¹ induced by external stimuli. The movements may be induced by light, gravity, moisture or contact with foreign bodies and accordingly may be termed as *phototropism*, *geotropism*, *hydrotropism* and *thigmotropism*.

In all the cases of tropism, direction of response of the organs bears a definite relation to the direction of stimulus—either towards or away from the stimulus. Accordingly, the movement is said to be *positive* when it moves towards the stimulus or *negative* when it moves away from the stimulus.

(i) **PHOTOTROPISM**—It is the *phenomenon of orientation and direction of movement of plant organ where incident rays or light act as stimulating agent*. When light comes from only one direction the

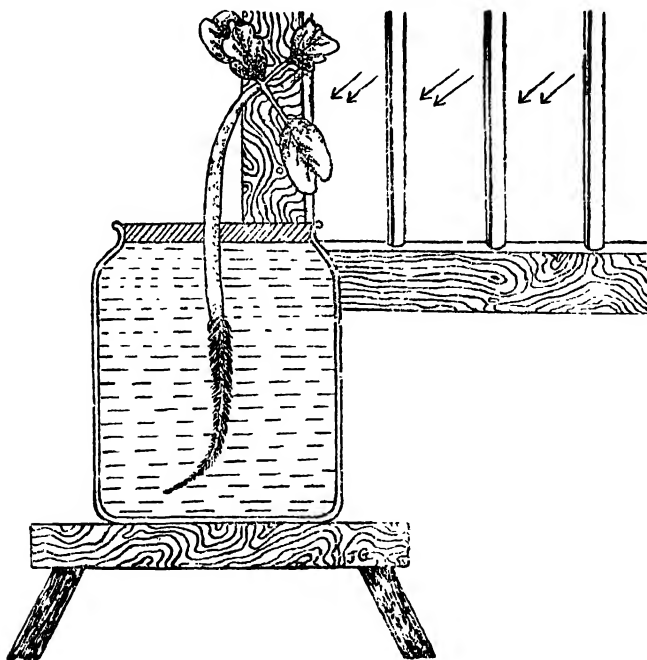


Fig. 20.1 Arrangements showing the phototropic response in a plant.

shoot usually bends towards the direction of more intense light, whereas the root moves away from the source of stimulus (Fig. 20.1).

¹ They are caused by change in the position of organs due to enlargement of cells or increase in the number of cells or both.

So under these circumstances the shoot is *positively phototropic* and root is *negatively phototropic*.

Phototropic curvatures are very familiar to us. They are specially conspicuous in plants growing in a place subjected to unequal illumination.

Hormonal concept of phototropism—Phototropism may be explained due to unequal distribution of auxin on two sides of the stimulated stem. The auxin which is produced at the tip of the stem, diffuses downward to the zone of elongation, where it accumulates, usually on the sides of the stem depending on the direction of light. This accumulation of auxin is based on the fact that :

(i) Strong light inhibits the formation of auxin on the illuminated side so that the shaded side accumulates more auxin and (ii) an oblique translocation of auxins from lighted region to the shaded region takes place under the influence of light.

So due to greater accumulation of auxins on the shaded side of the stem there is a rapid enlargement of cells on the shaded side consequently bending the stem towards the light. In the root, however, the activity of auxins is just the reverse of stem. It requires a very low concentration of auxin for its activity and so the root cells placed towards the lighted side become more active (because of lesser amount of auxins). Thus the bending takes place in opposite direction (i.e. away from light).

This theory of phototropic curvature is now supported by a large number of experimental evidences from different workers. Thus

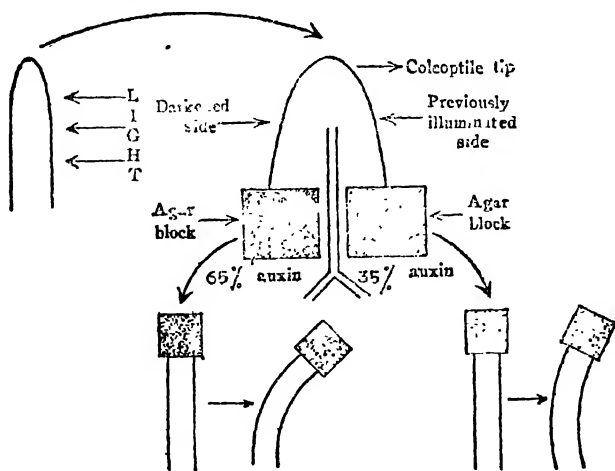


Fig. 20.2 Experiment of Went showing the more accumulation of auxin on the shaded side (65%) than the lighted side (35%).

by decapitating the coleoptile tip, the stems become insensitive to unilateral illumination. If however, the tip is replaced, normal

phototropic stimulus is restored. The obvious conclusion is that some chemical substances diffuse down from the tip to the region of elongation and then there is a differential distribution of auxins on the two sides of the coleoptile (Went, 1938). This can be demonstrated experimentally as follows. A decapitated coleoptile tip, after being subjected to unilateral light, is placed on two agar blocks separated by a piece of mica sheet so that the illuminated side of the coleoptile tip is placed on one agar block and the darkened side on the other block (Fig 20.2). When these blocks are placed separately on the decapitated coleoptiles, the agar block of the shaded side produce a greater curvature than the other agar block showing that more auxin accumulates on the shaded side than on the illuminated side. Quantitative estimation of auxin on the two sides of the stem also revealed that the shaded side of the coleoptile tip contained a greater concentration of auxin (65%) than the illuminated side (35%). If the tips are placed in the dark, the auxins are found to be uniformly distributed and it clearly signifies that unilateral light causes the redistribution of auxins and results in the subsequent curvature.

The positive phototropic curvature towards the incident light has been supposed to be due to unequal distribution of auxins on the two sides of the coleoptile. The farther side (away from light) has more auxin than the lighted side due to light induced inactivation or destruction of auxins in the lighted side. But it has been found that a solution of auxin (IAA) is perfectly stable in light. The effect of light cannot, therefore, be a direct one but must be mediated through light absorbed by some other pigment e.g. *riboflavin* (vitamin B₂) which occurs in many plant organs. Riboflavin involved in some way or other in the photodecomposition of auxins i. e. the light absorbed by riboflavin brings about the photochemical reaction, leading to the destruction of auxin. But another difficulty is that why does not riboflavin absorbed light, destroy auxins on both sides of the coleoptile in equal amounts as the coleoptile sheath is only 2mm thick? Most probably carotenoids prevent the destruction of auxin by light. With carotene present in the coleoptile, it may provide a filter which causes a suitable drop in light intensity across the coleoptile leading to a gradient of increasing auxin concentration from the lighted side to the darker side.

In the photosynthetic purple bacteria, the phototactic movements shown by them seem to be due to light absorbed by carotenoids.

(ii) **GEOTROPISM**—*Capacity of roots and stems to orient themselves with regard to the force of gravity* is known as *geotropism*. The roots grow towards the force of gravity and are said to be *positively geotropic*, whereas the stems which grow away from the gravity are said to be *negatively geotropic*. Thus, if germinating seedlings of bean, castor etc., are placed with their developing tap roots vertically upwards and the stems downwards it will be found that the roots will bend and grow downwards and the stem upwards as a response to positive and negative geotropism. It is of very common

occurrence that irrespective of position of seeds, the roots go down to the soil and the stems upwards.

Hormonal concept of geotropism—Geotropism is a growth movement i.e. due to unequal growth of the tissues of an organ and this is due to the unequal distribution of auxin. In the vertical position when the roots grow towards the soil and the stem away from it, the production of auxins at the tips of the meristems and their diffusion towards the base is uniformly equal all round the circumference. As a result of this, there is a uniform growth of stems and roots and thus they maintain their vertical position. When the tips are placed horizontally, accumulation of hormones (auxins) takes place more on their lower surface (i.e. the sides nearer to the stimulus) than to its upper surface (i.e. the sides away from the stimulus). This

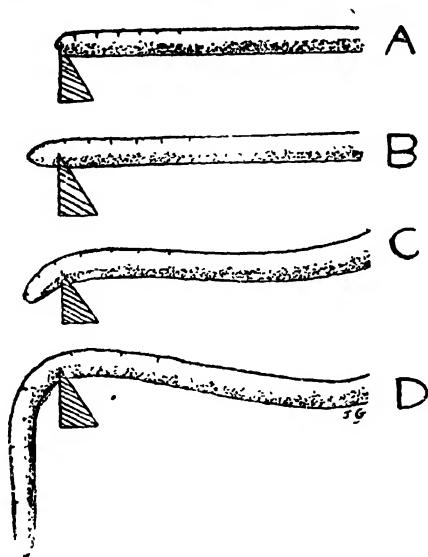


Fig. 20.3 Diagram showing the gradual course of a geotropic curvature. The arrow indicates a fixed index.

unequal distribution of auxins cause the unequal rates of growth on the two sides and produces a curvature. Since the roots are most effective at a lower concentration than stem, the activity is more on its upper side and consequently a curvature towards the direction of stimulus (Fig. 20.3). The increased concentration of auxin on the lower surface in stem causes an active growth on its lower surface and so a curvature on the opposite side in case of stem i.e. away from the stimulus occurs.

That the force of gravity acts as stimulus in bringing about geotropic curvature can be proved by removing the force of gravity. The neutralisation or removal of force of gravity can be done by

means of clinostat experiment (Fig. 20.4). A clinostat has a round disc that can be rotated horizontally either slowly or rapidly by means of a clock-work arrangement. A pot containing a seedling is fixed on the disc and the whole apparatus is placed in a horizontal position and the clock-work started. The disc containing the pot with seedling rotates along the axis slowly. Under these conditions all sides of stems and roots successively come to receive the geotropic stimulus equally. So no curvature of root or shoot occurs. If, however, the plant is kept in a horizontal position for some time without rotating the disc, the root and shoot show the characteristic curvature as shown previously.

Geotropic sensitivity is not quite constant and may be influenced by external as well as internal conditions, such as temperature. Owing to the effect of high temperature geotropism of stem may in some cases stop. Sugarcane stem fails to exhibit the normal geotropic

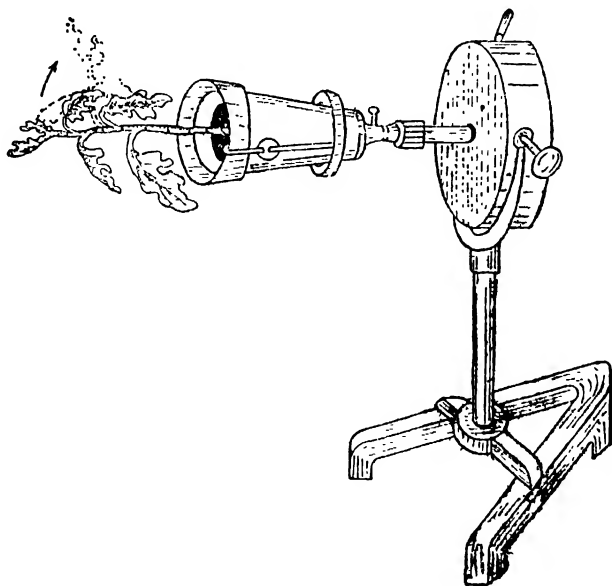


Fig. 20.4 A clinostat.

curvature if it is immersed in water at 52°C for about 20 minutes ; the warm water treatment reduces auxin concentration (van Overback, 1948) and so fails to exhibit the movement.

(iii) **HYDROTROPISM**—*The movement in response to the variation of water content is exhibited by the roots of higher plants.* And this is known as *hydrotropism*. Roots are therefore positively hydrotropic. The positive hydrotropic reaction of roots of seedlings can be demonstrated by placing them on moist hanging sieve containing moist sawdust. If the vessel is now inclined at an angle to the vertical axis

the roots instead of growing downwards by piercing the holes of sieve will bend and spread on the moist outer surface of the vessel in search of water (Fig. 20.5). Here the force of geotropism is overcome by

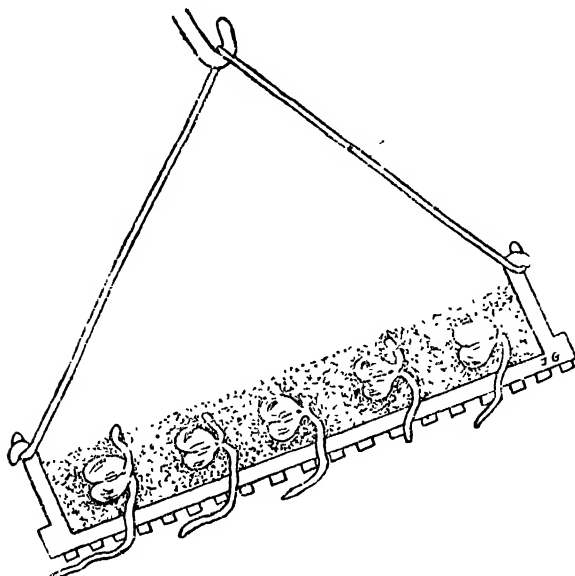


Fig. 20.5 Arrangement to demonstrate hydrotropism.

hydrotropism. These curvatures are caused by difference in the rate of enlargement of the cells on the opposite sides of the roots—although no definite proofs have been obtained.

(iv) **THIGMOTROPISM**—It is a phenomenon in which the movements by plants occur as a result of contact or touch with a foreign body. These movements are best exhibited by the growth of tendrils. As a result of unequal rate of growth the apices of young tendrils undergo nutation movements and make slow circular movements in elongation. Petioles of many species of plants, leaf-tip of *Gloriosa*, leaf-stalk of some species of *Clematis*, stipule of *Smilax*, leaflets of pea, branch of vine etc. are very much sensitive to contact with the foreign body and thus they execute the curvatures.

The cells of the tendrils that come in contact with a solid object accumulate auxins and the concentration is more on the sides away from the point of touch. This high concentration favours active cell division on the opposite side and consequently a short curvature is produced and the organ ultimately bends round the object.

The movement of the tentacles of *Drosera*, which was at one time thought to be purely chemotropic movement, has got a relation with the thigmotropic movement.

The roots also in some cases respond to the thigmotropic curvature. If the tip of a young root comes in contact with a stone it bends away from it. Thus the negative curvature helps the roots to avoid the obstacle in the soil.

20.3 Individual nastic movements—Nastic movements are induced paratonic movements in which the response i.e. the movement of plant organs, bears no relation to the direction of the stimulus. The stimulus acts on the protoplasm of cells from all sides. According to the nature of the stimulus nastic movements may be photonasty, thermonasty, chemonasty, nyctinasty, seismonasty etc. when the stimuli are light, temperature, chemical substances, both light and temperature and touch etc. respectively.

In nastic movement the direction of movement is not determined by the external stimuli. The response of the plant organ is always same from whatever direction the stimulus may come. In contrast to it the tropic movements proceed either towards or away from the direction of stimuli.

(i) *Photonasty*—The movements are concerned with the opening and closing up of flowers e.g. the flowers of *Pentaptes phoenicia* fully open at noon, whereas they close at night. The opening and closing of leaves of many Leguminous plants in day and night afford best examples of photonasty; in these, light from all direction acts as stimulus which causes opening and closing up of leaflets. Similarly, the leaves of *Oxalis* expand at day time and remain semiclosed and drooping at night. Light and darkness cause variation in turgidity of the cells of pulvinar tissues—hence the movement.

(ii) *Thermonasty*—The best example of thermonastic curvature is afforded by opening of flowers of *Tulipa*, where increase in temperature effects the opening of flower; consequent fall in temperature brings about closing of flowers. This is due to the change of turgor condition of pulvinus tissue.

(iii) *Chemonasty*—It is the movement induced by chemical substances. This type of movement is shown by insectivorous plants. If the soluble protein is placed in the centre of a leaf of sundew (*Drosera* sp.) then tentacles move towards it.

(iv) *Nyctinasty*—It is the most common of the nastic movements, where changes of temperature and light during the day and night induce visible response which may be termed as *nyctinasty*. Thus the opening and closing of certain flowers (e.g. cactus, tobacco etc.) are the examples of nyctinasty. Nyctinastic movement of variation due to changes of turgor in the pulvini is also exhibited by the leaf or leaflets of Leguminosae (e.g. clover, *Desmodium gyrans*, *Acacia*, *Bauhinia* etc.), Oxalidaceae (e.g. *Oxalis acetosella*) and also some species of fern and *Marsilea*.

This movement is controlled both by light and temperature. The individual factors acting singly may induce photonastic and thermo-

nastic movements. These movements are brought about by changes in the turgor of the cells of the pulvinus at the base of the petiole.

(v) *Seismonasty*—This phenomenon is observed in the movements of leaflets of *Mimosa pudica* (sensitive plants) as a result of shock, touch, shaking, pressure etc. When a leaf of *Mimosa pudica* is subjected to sudden touch or shock of any kind, the leaf and its parts droop down very rapidly, the leaflets close up, altogether presenting a new appearance. The leaves are digitately compound consisting of a main petiole which bears at its tip two pairs of paripinnate segments bearing secondary petiole.

On being stimulated the main petiole at once droops down, the secondary petioles at the same time close together, somewhat followed by simultaneously folding up of the respective leaflets, so that each pair of leaflets comes in close contact. The whole thing consists by three movements—movement of main petiole, movement of secondary petioles and the closing and folding up of respective leaflets. The bases of the main and secondary petioles are provided with pulvini consisting of loose parenchyma cells with intercellular spaces inside and the movements are brought about by changes in the turgor of the cells of pulvinus.

The rapid conduction of stimulus through the entire aerial parts of the plant and consequent response in the movements are very striking. After movements and consequent folding and closing up of leaflets there is slow recovery of the leaves in their former expanded position. According to J. C. Bose the latent time for seismonastic response in *Mimosa* is very short, being less than a second. According to Ricca the path of conduction of stimulus is vascular bundle and its associated cells. According to him as a result of excitation i.e., shock or blow, a substance perhaps a hormone is produced in protoplasm which diffuses into the xylem and phloem through water and on reaching pulvinus brings about the changes of turgidity. The turgor changes is mainly associated with loss of water from the cells of lower half of the pulvinus, the water passing into the intercellular spaces of parenchyma of the pulvinus.

Similar seismonastic movements are also afforded by stamens of many genera of Compositae (e.g. *Cynara*) when one filament is touched, contraction of other filaments results. The movements of leaf of *Dionaea* (Venus fly trap), etc. are all seismonastic.

20.4 Nutation—It is a special type of movement exhibited by the stem tips in course of their elongation, showing an irregular spiral path as they elongate. This phenomenon is known as **nutations** or **spiral movement**. It is due to some internal factors that affect the growth rate of plant segments.

The best example of nutation movement can be exhibited by the twinning plants. The stem tips of twinners are long and devoid of leaves. The stem tips have less mechanical tissues and thus the tip of the stem usually droops down in a horizontal position. As a

result of rapid growth of the stem there is a swinging movement of the tip. This observation has been affirmed by Charles Darwin, who showed that every plant, as it continues to grow, is continually nutating. Although no detailed information has been available regarding the effect of the external conditions on nutation. Darwin's observation, however, indicates that the increase in temperature leads to increase in the rate of movement.

Experiment to show nutation movement—Prepare a very narrow glass filament from glass tubing. Take a part of this segment (about 10 cm) and attach it vertically to the stem tip of a well growing potted plant by means of wax. Take a 2 cm square white paper, perforate in the centre and slip it through the glass filament to a position near the base. Now support horizontally a rectangular

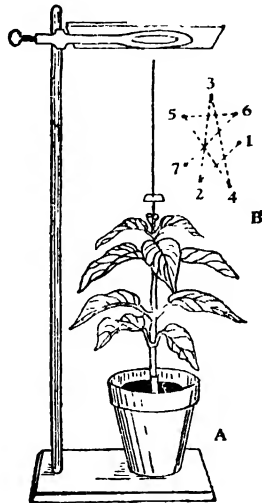


Fig. 20.6 Arrangements to show the nutation movement.
A—Complete arrangements. B—The direction of movements when pointed on the glass slab.

glass plate on a ring stand (Fig. 20.6, A) and adjust it in such a manner that the filament tip is just below the glass slab. Now looking down through the glass plate from top, place a dot of ink (Indian) at a point on the plate where the tip of the filament remains in the centre of the square white paper. Thus by plotting it at different interval of times, the direction of the movements can easily be observed (refer fig. 20.6, B)

20.5 Turgor movements—It is a type of movement caused by reversible change of cell size due to variation of the turgor of the cells. As the movement is dependant on the turgor pressure of the cells. it is known as turgor movement. It is quite different from growth movement¹ which involves the permanent increase in the number of cells in the tissue.

¹ It is a movement caused by the permanent increase in the size and number of cells in the tissues. All tropic movements, nastic movements, nutation include within the growth movement.

It includes the rolling of leaves in a number of grasses (e.g., *Poa pratensis*) during wilting, the so-called 'sleep movements' of the leaves during night and the spectacular movement that occurs in the sensitive plant (*Mimosa pudica*).

For detail discussion refer nyctinasty and seismonasty movements under article 20.3.

SELECTED QUESTIONS

1. What do you understand by autonomous induced movements in plants. Illustrate your answer with suitable examples.

Refer article 20.1, 20.1A and 20.1B

2. Write an essay on the tropic movements in plants.

Refer article 20.2

3. What is phototropism? Discuss the role of light-growth reaction and auxins in the tropic movements of plants.

Refer article 20.2 (i) and (ii)

4. Write an essay on nastic movements in plants.

Refer article 20.3

5. What do you mean by nutation? Describe the plant movements caused by nutation.

Refer article 20.4

6. Give an account of turgor movements in plants. Describe in detail the seismonastic movement in plants.

Refer article 20.5

7. What do you understand by plant movements. Write an essay on movements of plants.

Refer introduction of Chapter 20 and articles 20.1, 20.1A and 20.1B

8. Discuss the probable role of auxin in inducing geotropic and phototropic curvatures in plants.

Refer article 20.2 (i) and (ii)

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**ECOLOGY
AND
PLANT GEOGRAPHY**

CHAPTER I

Introduction

1.1 What is Ecology ? *Ecology* is the special term for the field of environmental biology, this term was employed first by a German ecologist H. Reiter in 1885. The term ecology is derived from the Greek word '*Oikos*' which means 'house' or dwelling place.

Thus ecology, literally, is the study of 'houses', 'home conditions', 'habitat' or more broadly 'environments' of plants and animals. According to Warming and others, plant ecology *is the study of plants in relation to their environment.*

1.2 Aims and Scope of Plant Ecology : Plants are found to grow in all environmental conditions over the surface of the earth ; some grow on high mountain tops, some round hot springs. They also grow in deserts, dry rocks, moist places like river banks and marshy areas, majority growing in normal conditions on plains although some are found to grow in the crevices of walls and tree trunks. Owing to these diverse habitats, plant behaviour is also regulated by the environmental conditions—such environmental factors have great effects, either singly or collectively, upon those plants. Plant ecology, of course, comprehends all such phenomena.

Naturally, the behaviours of plants are regulated and controlled by the environmental conditions and the biological forces i.e., forces of heredity working within ; as both environment and plants are dynamic systems reacting on each other, so the resultant organisms i.e., plants have much potentiality for change. The different factors of the environment play an important role on the organisms like plants which may get modified.

At present the scope of ecology is vast and useful in the realm of applied sciences. It is actually one of the main lines of advancement as ecology is becoming applicable to more and more aspects of agricultural sciences and in different fields of human endeavour. The ecological problems have direct connection with soil conservation, flood control, deforestation, orcharding, town-planning etc. A concrete example, taken out of the hectic efforts in commercial and agricultural enterprises, will clarify this—gradual deforestation of land has affected and will affect the timely appearance of the monsoon with a resultant disturbance in the cycle of seasons and hamper cultivation. Further, ruthless destruction of rooting shrubs, seedlings and trees on river-banks causes land erosion.

Scope of ecology is also associated with argonomy and horticultural science, e.g. soli-biotic factors are intimately connected with agriculture and horticulure. Furthur, in regard to field methods, workers in agricultural research whose problems are largely ecological are dependent on ecologists.

Ecology needs field study which consists of recording and examining different plant species growing in a vegetation-covered area and the estimates and accounts are made of the environmental conditions under which plants are growing. Ecology is one of the basic divisions of biology like physiology, genetics, mycology etc. and as such ecology is an integral part of those divisions dealing with specific groups. Plant ecology is also closely associated with plant geography and plant taxonomy. The problems involved in the study of plant ecology require investigations of different habitat factors and estimation of intensities regarding those factors which affect the plants physiologically.

1.3 Divisions of Ecology : Ecology is divided into two major divisions viz., (a) *autecology* and (b) *synecology*. Ecological study of individual species or plant is called autecology while the study of "a *population* of species growing together" or plant communities is called synecology.

Bio-ecology is a term applied to synecology when synecological study of both plants and animals is considered. There is another terminology e.g., plant-sociology which means the "community relationship of plants"; this term is sometimes used for synecology.

Origin of Vegetation and Life-form (Growth- form) of Plants

Vegetation of a particular area is the total aggregation of various plants having different life-forms like large and small trees, shrubs, lianes and cryptogams including mosses, ferns, algae, fungi etc. growing in that area. Vegetation of a particular area depends upon the interactions of various factors, such as, the effects of plants on the region in which they grow and live, the influence of plants themselves on each other etc. In a particular forest, tall trees generally exert influence on the growth of other plants of low stature, e.g., herbs shrubs etc., by arresting some light, decreasing the force of wind, checking the soil evaporation by the fallen leaves on the forest floor etc., so sun-loving shrubs or herbs gradually disappear and are replaced by the plants that can thrive in cool, moist and shady places. In this way outcome of new vegetation in an area takes place.

Plants inhabiting a particular area or region have various types of life-forms. As species are units in plant taxonomy, so life-forms are units in ecology. In a broad sense, life-form means the characteristic vegetative appearance such as size, shape, branching and also the anatomical features of plant body and its longevity. Strictly, life-form "refers to the forms based on the location of the overwintering parts." According to Hanson and Churchill (1965) life-form of a species is caused primarily by its genetic constitution and secondarily by environmental conditions. The life-form influences the economic value of plants in various ways, it has got also considerable influence on the association of species. Various types of life-forms in an area inhabited by different kinds of plants have been classified by different authors. According to Warming (1909) life-form (growth-form) may be arranged into following six main classes, namely :—

1. *Heterotrophic growth-form*—shown by all holosaprophytes and holoparasites.
2. *Aquatic growth-form*—shown by hydrophytes.
3. *The Muscoid growth-form*—characterised by mosses.
4. *The Lichenoid growth-form*—exhibited by lichens.
5. *The Lianoid growth-form*—characterised by lianes.
6. *All other autonomous land-plants*—this class includes the growth-forms adopted by all the remaining autotrophic land

plants which contain chlorophyll—the growth-forms of pteridophyta and spermatophyta are included in this class.

All the above main classes, specially the growth-form of the autotrophic plants belonging to sixth class, are again divided into sub-classes, e.g.

Sub-class I Monocarpic herbs—it includes following groups :—

- (a) *Aestival annual plants*, (b) *Hibernal annual plants* and (c) *Biennial-perennial herbs*.

Sub-class II Polycarpic plants—it includes following groups :—

- (a) *Renascent herbs*, (b) *Rosette plants*, (c) *Creeping plants* and (d) *Plants with erect long-lived shoots*.

Of the many classifications that have been proposed, Raunkiaer's (1934) system is the most widely known and accepted. His classification of life-form of plants is as follows :—

1. *Parasites and Epiphytes*.
2. *Plants with succulent habit*.
3. *Climbers and twiners*.
4. *Trees and shrubs—phanerophytes*.
 - (a) Tall trees—*megaphanerophytes* (plants more than 30·5 m in height).
 - (b) Trees (height ranges between 30·5 m and 7·5 m)—*meso-phanerophytes*.
 - (c) Trees and shrubs (height ranges between 7·5 m and 1·8 m)—*microphanerophytes*.
 - (d) Shrubs (height ranges between 1·8 m and 0·25 m)—*nanophanerophytes*.
 - (e) Undershrubs or herbs with vegetative buds not more than 0·25 m above the soil surface—*chamaephytes*.
 - (f) Plants with vegetative buds on the soil surface—*hemicryptophytes*.
 - (g) Plants with buds deeply buried in the soil and on the underground stem—*geophytes*.
5. *Annual herbs—therophytes*.
6. *Water and Marsh plants*—plants with buds under water—*hydrophytes* and *helophytes*.

According to Raunkiaer, forest communities are dominated by all types of *phanerophytes*, deserts by *nanophanerophytes* and *chamaephytes*, and grassland by *hemicryptophytes*. Temperate vegetation (arctic and alpine) is dominated by *chamaephytes*, aquatic vegetation by *hydrophytes* and *helophytes*. *Geophytes* generally dominate on soft and loose soil. *Therophytes* dominate mainly on open soil, seashores and in most watery places.

Braun-Blanquet (1951), on the basis of Raunkiaer's classification, classified life-form into following ten main classes :—

1. *Phytoplankton*—microscopic plants suspended in air, water, or on snow.
2. *Phytoedaphon*—microscopic soil flora.
3. *Endophytes*—plants living wholly or partly within other plants, as algae in lichens, or parasites.
4. *Therophytes*—annuals, including algae, fungi, liverworts, mosses, many ferns and seed plants.
5. *Hydrophytes*—all water plants, except plankton, with perennating parts submerged in water during unfavourable periods.
6. *Geophytes*—plants with perennating parts buried in the substratum, such as species with rhizomes or bulbs.
7. *Hemicryptophytes*—plants with perennial shoots and buds close to the surface, often covered with bunch-grasses and many forbs (nongrassy herbs).
8. *Chamaephytes*—plants with buds located from the soil surface to 25 cm above it.
9. *Phanerophytes*—shrubs, trees and vines with buds located on upright shoots at least 25 cm above the soil surface.
10. *Epiphytes*—plants growing on other plants.

Most of the above mentioned classes have been divided further. In a particular region or in a community, all the species may be classified into these classes and the ratio expressed in numbers or percentages forms a floristic *biological spectrum*. According to some authors, the phenotypic growth-form is a part of the life-form. Such growth-form refers to the development of plants of the same species under different environmental conditions.

Ecological Factors

Ecological or *habitat*¹ factors are the various conditions which affect the growth of plants and determine the nature of plant communities. These ecological factors have been grouped by most of the authors² under (1) *climatic factors*, which include conditions like temperature, light, wind etc. of the region where the vegetation is situated; (2) *physiographic factors*, which include those resulting from topography of that area; (3) *edaphic factors*, which include the effects of soil conditions in relation to vegetation and (4) *biotic factors*, which are the various effects resulting from the vital activities of animals and of plants themselves.

3.1 Climatic Factors : These are the factors of habitat, which are concerned with and influenced by precipitation (rainfall, snow, dew etc.), atmospheric humidity, temperature, light, velocity of wind etc. The behaviour, duration and intensity of those factors constitute the climate of a region or habitat. Some authors differentiate climatic factors into *microclimate* or *microenvironment* and *macroclimate* or *macroenvironment*. The microclimate is strictly restricted to localised area. Hence microclimate refers to local combination of atmospheric factors, which due to local variations in the climate, topography etc. differ from the prevalent general climate i.e. macroclimate of the region. Macroclimate is the general atmospheric condition of a region.

(a) *Precipitation*—It determines the type of vegetation in particular areas. The main-types of precipitation are rainfall, snow and dew. Of these, rainfall is most important as it affects the growth of plants, distribution of plants regarding types etc.—so rainfall of a place has direct influence on vegetation. With the increase of rainfall atmospheric humidity is increased—it acts indirectly through the medium of other factors like temperature and light. Mosses, ferns, lichens with ever-green trees abound in an area with heavy rainfall; whereas tropical countries with low rainfall are reckoned as arid regions—there the vegetation is sparse. Rainfall with seasonal periodicity of restriction brings about more change in vegetation than constant rainfall in a particular area. Seasonal restricted rainfall results in growth of few species whereas, constant rainfall with cloudy sky almost throughout the year favours the formation of tropical rain forest with abundance of species with lianes, ferns, epiphytes etc. On the basis of seasonal distribution of rainfall, there are three main types of vegetation *viz.*, forest vegetation, grassland vegetation and

¹ According to W. Leach (1949)

² R. F. Daubenmire (1959) has, however, classified environment in relation to vegetation into seven headings *viz.* (1) soil, (2) water, (3) temperature, (4) light, (5) atmosphere, (6) fire and (7) biotic factors.

desert vegetation. In warm countries where annual rainfall is heavy althrough, only the formation of forest vegetation takes place there. Lighter rainfall (where rainfall is heavy during summer but low during winter) is responsible for the formation of grasslands. Regions with very low rainfall both in summer and winter correspond with deserts.

According to Schimper, (1903, '35), "the type of vegetation (both in tropical and temperate regions) is conditioned by the total amount and seasonal distribution of rainfall and by the humidity of the air."

(b) *Atmospheric humidity*—Humidity of the air has a great influence on plant life, as it affects the water relations of plants. The rate of transpiration is directly influenced by atmospheric humidity. Water vapour present in the air is responsible for humidity, and the concentration of water vapour is greatly controlled by temperature. Atmosphere i.e. air can hold maximum amount of water vapour at any temperature, and at that temperature the actual pressure of water vapour (absolute humidity) as expressed by percentage of the maximum is called *relative humidity*. The difference between the absolute humidity and relative humidity expresses the saturation deficit of the air. Saturation deficit is directly related with the evaporating power of the air and thereby largely controls the rate of transpiration. The rate of transpiration is higher if the relative humidity of the air becomes lower. Atmospheric humidity is increased owing to precipitation, soil evaporation and plant transpiration. Hence in a dense vegetation, the air beneath the vegetation is more humid. In humid regions, moisture-loving delicate plants generally grow and such plants become more elongated with long internodes and thinner leaves.

(c) *Temperature*—It plays an intensive role in plant organisations, as vital activities in plant life are confined between maximum and minimum temperatures. Before maturation, each crop plant requires a certain number of "effective heat units"—this is called *thermal constant* which varies with different crop plants. The temperature and the length of the vegetative season affect the physiognomy of the individual plants and also the whole of the vegetation. Temperature also exerts an influence on habitat, economy and struggles of plant communities.

In a country with low average temperature the vegetation cannot be similar to that of a country having average higher temperature ; so temperate and tropical flora differ in species, physiognomy etc. This is due to heat exerting an influence on habitat, growth formation etc. of a plant community.

In the equatorial region where high temperature is linked with humidity, evergreen tropical luxuriant vegetation develops with dense crowding of species. In tropics where high temperature is associated with drought (i.e. dryness) dwarfish growth, shrubby heath-like formation result ; control in the loss of water i.e. check to transpiration associated with sunken stomata, thick cuticularised leaves,

reduction of leaves by spines etc. is found in plants growing in the region. In Arctic and Alpine climates where temperature is very low and the favourable period for blossoming is very brief, annual plants are rare ; there perennial herbs with long resting period and varieties of forms are common.

There are different types of plants which can withstand different temperatures. According to some authors entire geographical distribution of plants depends on varying temperatures e.g. tropical plants require constant high temperature for their maximum growth, the Alpine plants require very low temperature and are adapted for short summer period for flowering, fruiting etc.

(d) *Light*—Light is one of the most important factors from the stand point of physiological processes. Light is directly concerned with the growth and development of plants as it helps in the formation of growth hormones, chlorophyll etc. Synthesis of food by green plants and the process of transpiration also depends upon light.

Light affects plants by its intensity, quality and duration. Light intensity is influenced by altitude and humidity—e.g. light intensity increases with altitude while humidity reduces light intensity. Intensity and duration of light play important roles in the construction of vegetative shapes of plants—this is seen in the different shapes of sun (*heliophytes* or photophilic) and shade (*sciophytes* or photophobic) plants. The characteristics of these plants are as follows :—

(i) Intense or strong light retards the growth of shoot.

(ii) Sun plants have short internodes and small narrow leaves while shade plants have long internodes and large leaves.

(iii) Sun plants are shorter and stockier than shade plants.

(iv) Sun plants have thick and small leaves ; leaves are often stiff and coriaceous with distinct veins. Cuticle of leaves is very thick and waxy ; palisade tissue and vascular tissues are well developed, spongy cells are more or less poorly developed.

Shade plants have soft and succulent leaves, veins are small—their leaves are thinner but larger and broader, and without well developed cuticle. Palisade tissue is practically lacking, spongy cells are well developed.

(v) In sun plants lignified tissues are well developed ; cells are smaller with less intercellular spaces. In shade plants lignified tissues are poorly developed, cells are larger with intercellular spaces.

(vi) Sun plants have dense covering of hairs while shade plants are less hairy.

(vii) Shade plants are delicate and without any well developed mechanical tissues. Sun plants are not delicate, their mechanical tissues are well differentiated.

(viii) Plants growing in shade become etiolated, their stems are often weak and pale yellow, while sun plants have stout green stems.

(ix) The stems of shade plants are taller and more branched than that of sun plants.

Formation of flowers, fruits and seeds is favoured by intense light. Duration of light period, i.e. *photoperiodism* has marked influence on growth, flowering and fruiting to plants. In nature, duration of light period varies from less than twelve hours or twelve hours (on the equator) to more than twelve hours during summer (in Arctic regions). The quality of light e.g. red, blue, ultra-violet rays of light also influences the growth and development of plants. Red rays generally induce the greater development of tissues and thereby cause the cells to enlarge. Blue-violet rays, on the other hand, inhibit the growth and enlargement phases of cells. Ultra-violet rays have injurious effect upon the growth of plants.

(e) *Velocity of wind*—It has both direct and indirect effects on plant life. The direct effect of wind is mechanical, strong wind is responsible for uprooting trees and breaking off branches, twigs etc. Wind also exerts influence on structure, strong wind coming from one direction affects tree growth and form ; those trees, subjected to one-sided high wind, are low with bent trunks and short shoots which irregularly branch. The indirect effect of wind is physiological. Owing to violent wind, desiccation due to transpiration takes place ; so the growth of the axes and leaves is hampered or decreased.

3.2 Physiographic or Topographic Factors : Topographical relief of a country including variation in *altitude, steepness or slope of rock, exposure, direction or placement of mountain valleys* etc. can influence vegetation by bringing about variation within those factors.

Altitude affects vegetation in bringing about climatic changes due to changes in atmospheric pressure, which has direct influence on changing the humidity of air. Further, reduced pressure with increase in altitude causes lowering of temperature and consequently affects transpiration.

Position of a slope with respect to sun's rays also affects humidity through the action of sun and wind, the effect of wind being marked on slopes. The summits of mountains and hills are occasionally enveloped with clouds—this results in frequent rainfall, affecting vegetation. The slope also causes variation in water content of the soil in addition to its determining the character of the soil.

Type of vegetation is largely determined by the *exposure of slope*. A slope exposed to wind and sun has different vegetation from that of a slope which is not exposed to either.

3.3 Edaphic Factors : Edaphic or soil factors constitute all conditions of soil regarding mineral and organic matter contents

capacity of retention of water, humus content, temperature, air of soil etc.—these soil conditions determine the types of vegetation in an area.

(a) *Water content of soil*—Soil contains some amount of water. In different soils, that amount varies ; accordingly soil is classified as (a) very dry, (b) moderately dry, (c) very moist, (d) moderately moist, (e) wet and (f) very wet. Rain is the main source of soil water. After heavy showers, some amount of water runs along the slope forming *run away water* ; some of the water percolate owing to gravitational force, this is called *gravitational water*. But much of the rain water is retained by the soil particles against gravitational force and as a result the soil becomes wet, such type of water absorbed by colloidal soil particles is called *hygroscopic water*. Certain amount of water also remains between the spaces of non-colloidal soil particles forming *capillary water*. The water-holding capacity or field capacity of the soil includes both the hygroscopic and capillary water—it varies according to the texture of soil, e.g. coarse sand retains 10% of water of its dry weight, loamy soil may retain 35% of water and clayey soil retains a little higher. Water-retaining capacity of the soil is also dependent on percentage of organic matter, size and compactness of soil particles. Formation of adventitious roots and prostrate habit is favoured by moisture in the soil.

(b) *Soil temperature*—This factor has a significant effect on growth-forms of plants. High temperature in soil favours the development of thick roots, stems and leaves. If soil temperature falls below an optimum or minimum, then functional activities of roots i.e. absorption of water and nutrient salts decrease and plants ultimately wilt. Nanism i.e. dwarf, growth-forms result from low soil temperature ; cold soil favours the prostrate habit, rosette growth-form etc. whereas warm soil induces the tall and slender growth-forms. The activity of soil micro-organisms also depends upon favourable soil temperature.

(c) *Soil air*—Air in the soil is also an important factor as the habit and internal structure of plants are correlated with the amount of air the soil contains. Normally soil has a porous structure ; porous soil contains air and water between the inter-spaces of particles. The aeration of soil depends upon the porosity i.e. pore size of the soil. Soil air is very essential for the respiration of underground plant parts and soil micro-organisms. Soil fertility is also dependent on the soil air as soil air is necessary for breaking down of insoluble minerals into soluble salts and humus formation. Germination of seeds, growth and development of roots, absorption of water and salts by roots etc. all require oxygen available from the soil air. Very wet soil is poor in oxygen ; hence in this soil, plants having larger air spaces can thrive. Water-logged soil contains very little oxygen and high carbon dioxide ; under this condition, due to the anaerobic respiration of underground plant parts and micro-organisms, toxins harmful to plant growth are produced.

(d) *Soil reaction*—The growth and formation of plants depend upon soil reaction. According to the percentage of hydrogen ion concentration (pH) in soil solution, soil reaction is either acidic or alkaline. The pH value of water is 7, i.e., neutral; any value below 7 indicates acidity and above 7 indicates alkalinity. Normally, the basic soil reaction is due to the presence of free calcium carbonate. Extremely acid soil has pH value between 3 and 4; this soil is also called 'sour' soil. Acid soils are generally deficient in calcium. In this soil some acidophilous (acid-loving) plants like *Rhododendron*, *Shorea robusta*, *Vaccinium*, *Pinus roxburghii*, species of *Sphagnum* and *Polytrichum* can thrive well. Plants like some genera of mosses, *Trifolium*, *Anthyllis* etc. can thrive only in soils rich in lime or calcium—those plants, growing only in alkaline soil, are known as calciphilous (lime-loving) or acidophobic (acid-fearing). Soil acidity has also got harmful effects—acidity decreases the activity of nitrifying and nitrogen-fixing bacteria, earthworms etc.; it also helps in the accumulation of CO_2 and other toxic substances. Sometimes soil contains high concentration of soluble salts (e.g., carbonates of sodium and potassium chlorides and sulphates of sodium, potassium, calcium etc.); such saline soil is known as *alkali soil*. Alkali soils are of two types, viz. (a) *black alkali* in which black or dark-brown incrustations on the soil surface are formed, and (b) *white alkali* in which white incrustations are formed on the soil surface. In saline soil only a particular vegetation i.e., halophytes can thrive well, while growth of other vegetation like crop plants is adversely affected.

(e) *Organic matter in the soil or humus*—Humus is the organic matter in the soil derived from the decay of the dead remains of plants and animal parts. It is a dark-coloured, amorphous and relatively inert substance. The dead plant and animal remains decay, i.e., their bodies are broken into humus (or humine) by the activity of soil micro-organisms and are then gradually mineralised into molecular or ionic forms which again can be absorbed by living plants. All soil contains humus, humus is the part of the soil organic matter which is structurally nonrecognisable, colloidal in nature, and together with clay, forms a substance which is pedologically known as the *colloidal complex* of the soil. Greater part of the soil organic matter is derived from dead plant remains. They are either completely oxidised by bacteria into simple inorganic compounds, mainly CO_2 and H_2O by *oxidative decomposition* process or are converted into humus by *humification* process. Soil porosity and soil aeration are greatly influenced by humus contents of the soil—in this soil the root system is well developed. Humus soil favours the growth and formation of saprophytic plants.

(f) *Soil texture*—Soil is composed of mineral particles, organic matter or humus, soil water containing dissolved inorganic and organic substances and soil air. Inorganic or mineral particles are derived from the disintegration of rocks. The physical nature of the soil and its effect upon vegetation is greatly influenced by the size and

type of mineral particles of soil. Soil particles vary greatly in size and texture ; on the basis of which, soil may be classified as follows :—

(i) *Gravelly soil*—This soil contains large particles (above 2 mm in diameter) of rocks (from which they are derived) together with sand (both coarse and fine) and silt. In gravelly soil, percolation of water and aeration are free. Lithophytes and many xerophytes form the main type of vegetations of this soil. Mosses, lichens and many algae are found to grow into lithophytes. Besides, many shrubby angiospermic perennials such as grasses with deeply penetrating roots are developed.

(ii) *Sandy soil*—Sandy soil is mainly composed of sand particles, the diameter of which varies between 2 mm (coarse particles) and 0.2 mm (fine particles). Sandy soils are light, loose and poor in nutrients. They have poor water retaining capacity and as such, they dry up quickly and become heated in sun light. The vegetation is mainly xerophytic. Annual and biennial species are common. The important species are *Ipomoea biloba*, *Spinifex littoreus*, *Festuca ovina*, *Eryngium maritima* etc. The roots are very long and profusely branched ; leaves have waxy coating. Thorny bushes, xerophytic perennials with long roots and long branched stolons are characteristics of sand flora or *psammophytes*. Biennial hibernating species e.g., *Cerastium semidecandrum* (Caryophyllaceae) also occur in sand-forming sand dunes.

(iii) *Clay soil*—Clay soil is mainly composed of clay particles, diameter of particles always less than .002 mm. This soil also contains particles of hydrated aluminium silicates. Clay soil is tenaceous, heavy and has great water holding capacity, particles have high cohesive power ; due to small interspaces between particles, aeration is defective. After prolonged drought, clay soil cracks and becomes very hard. Clay soil particles are negatively charged, due to this property they attract and bind positively charged particles or cations like K, Ca, Mg to their surfaces.

All types of mesophytic perennial or annual herbs with long horizontal rhizomes grow in clay soil. Many species of *Cyperus*, *Chenopodium*, *Marsilea* etc. form predominant vegetation in this soil.

(iv) *Silt soil*—This soil is practically intermediate between sandy and clay soils, diameter of particles ranges from .02 – .002 mm. Silt soil is also composed of fragments of rock-forming minerals. This soil shows the properties of colloids as it has a little tendency to absorb and hold water, aeration is more or less medium. Silt soils are most favourable for all sorts of vegetation.

(v) *Loam*—It is a type of soil composed of sand, silt and clay particles of different sizes ; in loam soil those particles are present in more or less equal proportions. Loam is the most suitable soil for the growth of majority of plants. Particles present in loam help greatly in proper aeration, water holding capacity etc. On the basis of com-

position of particles, loams are classified as *heavy* or *clay loam* (where clay particles are predominant) and *light* or *sandy loam* (where sand particles are predominant).

(vi) *Lime or Calcareous soil*—These soils are directly derived from limestones containing high amount (90-100%) of calcium carbonate (CaCO_3). Lime soil is very poor in nutrient contents, shallow and it contains surface humus containing calcium. It has great water-retaining capacity. Plants growing in lime soil have densely hairy covering, grey felt, often bluish green and more divided leaves, flowers having dull surface etc. Herbaceous type of vegetation is generally favoured in this soil.

(vii) *Saline soil*—Saline soil is rich mainly in sodium chloride (NaCl) and chlorides of other salts. This type of soil is confined to places near deltas and estuaries where tidal water enters from the sea. The vegetation is halophytic in characters. Of the trees and shrubs most plants belong to the family Rhizophoraceae; besides, herbaceous vegetation formation like '*Suaeda maritima* formation' is important in the Ganges delta.

3.4 Origin and Development of Soil : Origin and development i.e., formation of soil is a very slow but a continuous process. Of the climatic factors, rainfall acting over a long period of time plays an important role for successive changes in soil development. Under warm and humid conditions, weathering of rocks takes place quickly—as a result soils get leached of basic materials like lime. But again, in arid or semi-arid conditions, soils retain some amount of basic compounds like chlorides, carbonates, bicarbonates and sulphates of sodium, magnesium, calcium etc. Due to weathering processes, rocks are broken into small particles and some changes also take place in the chemical composition of the original material. Again, the loss of valuable plant food and the incorporation of plant and animal remains takes place by the leaching action of water.

There are several successive stages in soil development—these stages are called *infancy*, *youth*, *maturity* and *old age*. In the beginning all soils are formed from rocks by the combined action of several agents. Firstly, due to mechanical weathering process, rocks undergo fragmentation into larger and smaller pieces—this process takes place by geological agents like alternate freezing and thawing of moisture in the ground, erosion by wind and running water and surface scouring by glaciers. Secondly, decomposition or corrosion by the chemical weathering process of oxidation, reduction, carbonation, hydrolysis, hydration etc. of the particles takes place; besides, various kinds of bacteria, algae, lichens secrete acidic substances which also promote chemical weathering. In this stage soil materials, under the influence of percolating ice or rain water undergo solution. Next, organic matters, derived from plant and animal residues, are added in the soil and thereby soils become darkened and they are composed not only of mineral matters but organic matters.

When soil gets positional stability for a longer period, they attain maturity and old age. But in some cases, the soil does not attain maturity and old age due to some reasons e.g., in steep Himalayan regions, land slides and avalanches sometimes move masses of rocks and other parent materials; in deserts, soil is often subject to fresh deposition of wind-blown sand; in flooded areas also, the soil is subject to frequent deposit of fresh alluvial materials—in all these conditions, therefore, soils always remain youthful in stage of development and thus never reach old age or maturity. Soil texture and differences of relief also play an important role in soil formation—water is drained off from high-lying spots to lands and depressions and the soil, thus formed, at high levels is generally coarse-grained and dry whereas that formed in low levels is clayey and wet.

During the developmental period of soil, upward and downward movements of water due to various factors such as climate, living organisms, topography etc. bring about the transport of various soil constituents from one soil horizon to another—as a result, the soil assumes a stratified structure which can be seen if a vertical section of it is examined. Such a vertical section is called a *soil profile*. Soil profile is very important as it shows the stages of development reached by the soil and it gives much information regarding the nature of the soil forming processes in operation. Soil profile is made up of a succession of horizontal or stratified layers (termed *horizons*) of varying thickness which can be differentiated on the basis of structure, texture, colour etc. Strictly speaking, soil profiles consist of three distinct horizons viz. *A*, *B* and *C*. Horizon *A* forms the upper i.e., *eluviated* one, made up of the surface soil of the plough layer. *B* horizon is the layer next below, this horizon is known as *illuvial* horizon. In this horizon, part of the products leached out from *A* horizon by the action of percolating water i.e. by *eluviation process* has been deposited. This horizon is also termed as sub-soil. Immediately below it, lies the *C* horizon made up of weathered parent material in the upper part and unweathered rock below. Of the three horizons, only *A* and *B* horizons form the true soil or *solum*. The *A* and *B* horizons again may each show stratifications—the strata being indicated by the signs A_0 , A_1 , A_2 , B_1 , B_2 etc.

The soil horizons are composed of solid, liquid and gaseous materials. The solid portion is made up of inorganic substances derived as a result of the mechanical and chemical weathering of parent rocks and organic substances derived from living plants and animals and their remains. The liquid content of the soil consists of water, containing dissolved mineral matters. While the gaseous components of the soil are carbon dioxide and oxygen which occupy a portion of the pore space.

The character of the soil profile depends mainly upon climate i.e., a cool wet climatic region has moist soil, in which large amount of rain water falls but the evaporation is slow and the water moves through the soil in downward direction. Again in dry and warm

climatic region, the soil contains little amount of water ; in this case water moves in both upward and downward directions so that definite eluviated and illuvial horizons may not develop.

Again, the rate of the soil development and the course followed in the process depends greatly on the nature of the original substratum. Hard rock weathers slowly, consequently there will be slow soil and the vegetation formation on its surface. If the substratum is soft, rapidly weathering rock, soil and vegetation development will be relatively rapid.

3.5 Biotic Factors : Biotic factors constitute the effects of the activities of living organisms viz. plants, animals and soil micro-organisms like bacteria. The effects of biotic factors include interactions amongst plants growing in a community, between plants and animals including man and between plants and soil micro-organisms. They influence vegetation particularly in their changes.

Grazing by animal on a particular area causes change in vegetation. Vegetation of a particular area is damaged in various ways due to grazing by domestic animals—large number of plants is destroyed and many are trampled under foot, the soil texture and conditions are also disturbed. In India, forests are also being destroyed due to grazing by animals like cattle, goats, etc. ; they eat up most of the plants including tree seedlings on the forest floor, the soil is trampled and made hard and compact, and this becomes unfit for plant growth. Large animals like elephants, bison etc. cause great damage to forest trees by eating or uprooting them. Grazing by animals also causes change in vegetation e.g., grazing of pastures by goats, sheep etc. may develop vegetation dominated by thorny weeds whereas when that area is not grazed by those animals the vegetation is dominated by grasses and sedges.

In a densely populated area, one of the most important types of biotic factors influencing vegetation is due to man's multifarious activities—this is noted in farming operations. On badly farmed land, the vegetation possesses many natural features e. g., grasses and sedges grow tall and tend to spread beyond their limited area, presence of many unwanted i. e. useless plants, while on well farmed land only wanted plants grow and present an artificial appearance. This difference is mainly due to the fact that in badly farmed land biotic factors arising from human interference are less than in case of well farmed land. Change or destruction of vegetation by fire is another indirect biotic effect due to man's activities. In this operation, shallow rooted plants are fully destroyed while deep rooted plants and plants with underground stems are temporarily affected. These deep rooted plants and plants with underground stems grow up with full vigour following the first rains after the fire and assume dominance. Various interactions between different plants growing in a community also occur. In the soil there is competition for space, water, mineral salts etc. and in the air for light, oxygen etc. Due to

this competition or struggle for existence, more vigorous and well adapted plants become dominant while less vigorous and unadapted plants are suppressed. In this way dominant vegetation or community originates in a particular place, so competition exerts influence upon the distribution of plants to different regions.

Various types of soil micro-organisms like bacteria, protozoa, fungi, algae etc. play an important role in altering the physical and chemical properties of the soil and thereby increasing or decreasing the soil fertility upon which the nature of vegetation depends. Earthworms, snails etc. increase fertility in tunnelling the soil and thereby increasing the humus content. So animal activities also affect vegetation.

In many cases different plant groups (e.g., lichens), plants and bacteria (root tubercles of leguminous plants) live in mutual benefit—this is called symbiosis in which each partner derives some benefit from the other.

CHAPTER 4

Ecological Units or Units of Vegetation

4.1 Plant Community : One of the most characteristic features about plants is that they do not live alone in nature, instead they live together in a particular area forming small or large groups. In ecology, such groups of individuals of any one type of organism having a high degree of uniformity in composition and structure and occupying an area of essentially uniform environment is called *population*. Again all individuals of the populations constitute a *community*. So a plant community includes all plants of the populations in a given i.e., limited geographical area. Sometimes, a specific grouping of plants i.e., population is also termed *stand*, *community*, *concrete community*, *individual community*, *phytocenose* etc. (Hanson and Churchill, 1965). According to them, the term 'community' may also be used for any aggregation of plants. In a forest, trees growing together with ground flora, group of plants in a pond or lake etc. are all examples of different types of plant communities. In a community, plants of one or more species having same life- or growth-forms are more prominent than others due to their largest number—these species are called *dominant*. Generally a plant community is determined by the nature of dominant species it contains. As an instance, in a particular forest, several types of oaks, birches grow in addition to ground flora in large number, forming prominent appearance and thus they form dominant species of that tract ; in the sand community of Rajasthan desert, *Calotropis procera* and *Indigofera argentea* are dominant species. A community may be *close* or *open*—in open plant community, plants are growing apart from each other leaving open spaces so that new plants may migrate and settle ; in a closed community, no such bare spaces are left between the species so that new plant species may not migrate and settle.

A. Origin of Plant Community : All types of plant communities have their own origin,—they develop and mature ultimately. The origin takes place through several steps as follows :—

(a) Firstly, propagating organs of plants like seeds, spores, vegetative organs etc. are *migrated* from older plant communities to a new open area through some agents like wind, water, animals etc. —in this way *invasion* in an area begins.

(b) Next, only the surviving ones germinate in that new area and grow into mature plants ; these plants again reproduce and multiply

in that area forming a *colony*—in this way *colonisation* begins by the new and fittest individuals called *pioneers*.

(c) Then rehabilitation and adjustment of those migrants to a new land i.e. habitat take place—this is called *ecesis*.

(d) Further propagation of those plants in that area leads to the *aggregation*; due to aggregation, both interspecific and intra-specific struggle i.e. *competition* for food and space takes place—as a result some perish and some (stronger ones) survive. Then surviving plants interact on the habitat and change the environment through a process called *reaction*.

In this way, gradual but steady origin of plant community takes place due to the phenomena of migration, invasion, colonisation, *ecesis*, aggregation, competition and reaction. Finally the climate of a particular area will determine the nature of vegetation, whether herbs, shrubs or trees—on the basis of this the vegetation will be permanent and the final mature type is called *climax vegetation*. Hence the composition and population of the climax are determined by all factors of the mature ecosystem¹, but not by any one factor. According to Whittaker (1953) climax vegetation may be considered “as a pattern of populations corresponding to the pattern of environmental gradients.” With the alterations in those gradients (*clines*), the relationship among the populations changes.

B. Classification of Plant Community :

From time to time, plant communities have been classified by various ecologists. Schimper (1903) classified the communities, on the basis of climatic zones, into forests, grasslands and deserts. On the basis of water relations, Warming (1909) classified communities into hydrophytes, mesophytes, lithophytes and xerophytes. Clements, (1916, '28) classified communities in a different way. According to him vegetation occurs both in *climax* as well as in *developmental* units; to distinguish between the two units, he proposed the suffixation for climax unit and suffixes for seral or developmental unit. The climax unit is divided into formation and sub-divided into association while the developmental unit is divided into associates. The various terms used in the two units are discussed as follows :—

I. PLANT FORMATION²—Plant formation may be defined as a fully developed major kind of plant community within a climatic zone. The climax vegetation is also called formation. It is determined and controlled mainly by climatic and edaphic factors of the habitat. According to Misra and Puri (1954) “it is the product of climate and strictly delimited and controlled by it.” Plant formation may also be determined by biotic factors e.g. *anthropogenic formations* which develop through the continuous operations of man himself. When the formation is controlled by biotic factors, then the climax is generally called as *biome*.

¹ It is a functional unit where the biotic and abiotic components of the environment function together (for detail vide Chapter 6).

² This term was introduced by A.R.H. Grisebach in 1838 for the vegetative formation. *Linnaea*, 12.

Formation is mainly the product of the climate like rainfall, temperature, humidity etc. of the habitat. The climatic plant formations of the world are determined by the well marked types of climate prevailing over the greater areas of the earth's surface. Examples of this type of formation are tropical rain forests which occur all over the equatorial regions of the world, deciduous summer forests of Europe, N. America, eastern Asia etc. The edaphic soil formations are determined mainly by the nature of the soil e.g. tidal forest formations i.e., mangrove formations which are determined by saline soil.

Formation is the major ecological unit of vegetation. In India there are four main formations e.g. tropical, sub-tropical, temperate and alpine.

Generally three different types of formations are recognised viz. (a) forests, (b) grasslands and (c) deserts. Each formation is made up of one or several plant associations having definite growth-forms which impart a characteristic appearance e.g. a deciduous forest formation consisting of deciduous trees, whereas meadow or grass-land formation consists of herbs belonging to Gramineae mainly.

So long as the external climatic and other conditions remain same or almost same, a formation has on the whole, some uniformity in physiognomy (i.e. in general external appearance or growth-forms), although its floristic composition (i.e. species of dominant plants) may vary at different places, e.g. the forests of eastern and western Himalayas have the same physiognomy as both have same growth-form 'trees', but the two forest formations differ in floristic composition as for example, dominant species in one is *Quercus lineata* and in other *Q. dilatata*.

A formation may be simple, consisting of one type of growth-form e.g. phytoplankton formation consisting of floating small hydrophytes like *Wolffia*, *Lemna* mainly or a formation may be compound consisting of several associations e.g. tundra formation of N. America which is made up of (1) *Carex-Cladonia*, (2) *Carex-Poa* and (3) *Carex-Agrostis* associations.

The characteristic feature of a formation is the dominant and controlling species with definite growth-forms. The final and stable types of formation consisting of dominant species is called climax type of formation or simply *climax vegetation*. Champion (1938) has recognised following climax forest formation types in India and Burma. These forest formations are determined by well marked climate types prevailing over such areas.

1. *Tropical wet evergreen*—Burma, E. Bengal (now Bangladesh). Assam and a long belt in W. India.

2. *Tropical wet semi-evergreen*—Orissa and Andhra coasts, West Bengal, Assam, Bihar, Bombay, Mysore, Kerala, E. Bengal (now Bangladesh).

3. *Tropical moist deciduous*—Central and northern Burma.

4. *Tropical moist deciduous*—Northern Indian belt, Orissa extending upto C.P. (Madhya Pradesh).
5. *Tropical dry deciduous*—Central India.
6. *Tropical thorn forest*—Rajputana i. e. Rajasthan desert, Hyderabad, Sind and N.W.F.P. (Pakistan).
7. *Tropical dry evergreen*—On the coasts of Andhra and Madras.
8. *Sub-tropical wet forests*—Mysore, Madras, North Assam, North Burma and E. Bengal (now Bangladesh).
9. *Sub-tropical pine forest*—a belt from Kashmir to Assam and Burma.
10. *Sub-tropical dry*—N.W.F.P. (Pakistan) and Rajasthan.
11. *Wet temperate*—Sub-tropical Himalayas from N. Bihar to N. Assam and N. Burma.
12. *Moist temperate*—A sub-tropical Himalayan belt extending from Kashmir to N. Assam.

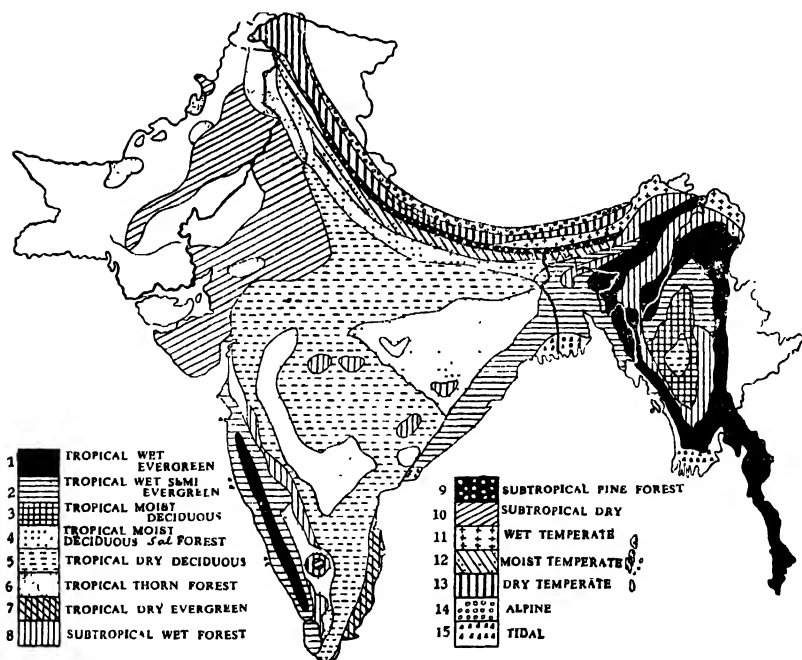


Fig. 4.1 Map showing the climax forest formation types of India and Burma (After Champion, 1938).

13. *Dry temperate*—A Himalayan belt from Pakistan (N.W.F.P.) right up to N. Assam, just below the alpine forest.
14. *Alpine*—Himalayan region above 3657.5m (≡ 12,300 ft).

15. *Tidal*—West Bengal (Sunderbans, Sagar Islands), Andhra (Godavari delta), Burma (Irawaddy delta), Andaman and Nicobar Islands and a very thin belt on Bombay coast.

II. PLANT ASSOCIATION—Association is a climax unit with two or more dominant forms. An association is also defined¹ as “the fundamental unit of phytosociology, being a plant community of certain floristic composition, of uniform habitat conditions and of uniform physiognomy.” The association in Clement’s idea is the main sub-division of a formation, generally two or more associations constitute each formation. In a formation, associations have the same physiognomy and more or less same floristic composition or slightly different floristic composition. Sometimes, association shows uniformity even in their floristic composition, at least with regard to dominant species. In the tropical zone of eastern Himalayas beginning from the plains upto an altitude of 1,000 m or so *Shorea robusta*, *Terminalia* species and species of *Garuga* are dominant and give rise to *Shorea-Terminalia-Garuga* association.

“*Associes* is a developmental equivalent of the association and being a seral or successional stage is replaced by other plant communities in succession.”

III. CONSOCIATION—It is a smaller unit of plant association i.e., climax community having a single dominant species. So an association may contain a consociation or as many consociations as depending on the number of dominant species, in the last case the name consociation is replaced by association. In a coniferous forest, there are several communities dominated by *Abies pindrow*, *Picea morinda* and *Pinus excelsa*,—here each of these communities is a consociation.

Consocies is a developmental community of consociation with a single dominant species.

IV. FACIATION—It is the sub-division of association which is related to minor differences in temperature and moisture relations. When in an association several dominants in two or more groups having almost the same physiognomy are present, then such association is called *faciation*. Forest vegetation of western Himalayas may be taken as an example, being an association of many species of *Quercus*, *Acer*, *Juglans regia*, *Castanea vulgaris* etc.

Facies is the developmental community equivalent to faciation.

V. SOCIETY—It is a part of an association “characterised by one or more sub-dominants.” Sub-dominants are mostly species of *different growth-forms* from the dominants, e.g. in a forest, sub-dominants are herbs, shrubs and other cryptogamic flora. The term “society” is generally used for ground flora communities.

Socies is a seral community equivalent to that of society.

Hanson and Churchill (1965) classified stand, community or concrete community into *community type*, *abstract community*, or *association*.

¹ By the Third International Botanical Congress in Brussels (1910).

According to them a community type or abstract community may be defined "as a group of stands that are similar in species composition and structure and occupy similar habitats." The association is a subdivision of the formation (Clement, 1916,'28) occupying a large area and recognised or delimited by its floristics, physiognomy etc. Hanson and Churchill think that such classification is valid and useful, specially within a limited geographic area. Stand *i.e.* individual plant community is the basic unit. Each stand has its own individuality and is marked by the possession of certain biotypes¹ and often ecotypes² also, which are not found in other similar stands. Delimitation of a stand results when it has sharp boundaries caused by abrupt changes or steep gradients (*clines*). In some places very small units of various types of vegetation occur repeatedly—such variations in species composition are caused by changes in the environment. Those small units are called *microstands*. The aggregate of such microstands in an area constitute *community-complex* when there is some pattern in distribution as on the edges of ponds or lakes, on sand dunes etc. But when the microstands are intermixed without any pattern, as commonly found in marshes and bogs, then the mass of vegetation together constitute a *community masaic*.

4.2 Plant Succession : Plant communities are not stable in a particular area ; instead, they are always changing from one type to another after their migration and occupation—they are born, develop and finally they become colonised by other groups of plants after maturity. This process of occupation of a particular area by different plant communities from their birth to maturity is known as *plant succession*.

According to Clement, "plant succession is the natural process by which the same locality becomes successively colonised by different groups or communities of plants." The occupation of an area from the beginning to the end *i.e.* climax or final stage is continuous and marked by a series of communities—these series of communities or in other words, intermediate stages (as seen between the beginning and the final stage) in the process of succession are called *seral communities* or *seral stages*, which together or as a whole constitute a *sere*. The final steady state or stage in the succession is known as *climax*.

It has been noted that in most of the cases, succession begins on primitive substrata *i.e.*, sterile area devoid of any vegetation *e.g.* a newly exposed sand dune or a recent lava flow—hence this type of succession is called *primary succession*. But when succession begins on areas previously occupied by well developed communities, or succession begins on areas where nutrients and conditions of existence of vegetation are already favourable *e.g.* abandoned croplands, plowed

¹ The population of a species within a given microhabitat may belong to one genotype, constituting *biotype*.

² Various clusters of biotypes, within one species, occupying a particular kind of habitat, constitute an *ecotype*.

grasslands, cut-over forests or new ponds, then that type of succession is called *secondary succession* or 'sub-sere'.

Succession may be *autogenic* or *allogenic*. In the former, the vegetation itself modifies the course of habit during succession. In the case of the allogenic type, some topographical conditions due to intense erosion or depositions are responsible for the course of succession.

According to Odum (1966), succession may be distinguished into two types e.g. (a) *autotrophic succession* and (b) *heterotrophic succession*. The former is the common and wide-spread type in nature which begins in a predominantly inorganic environment and is characterised and dominated by autotrophic organisms. Heterotrophic succession, characterised by heterotrophic organisms, occurs in special case where the environment is predominantly organic e.g. in a stream polluted with sewage or in a fallen log.

Depending upon the nature of habitats from which they originate, successions may be of several types. A succession which had its origin in watery habitats (i.e. marshy grounds, ponds, lakes, or any other aquatic environment) is called *hydrosere*. Similarly, a succession beginning in a dry area is known as *xerosere*, in saline water *halosere* and so on.

Succession is generally studied in two main types of habitats corresponding to the *sere* and the *climax*—the former is controlled by edaphic factors and the latter by climatic factors. Sere is an open habitat and climax is closed type. In seral habitat, invasion and colonisation take place while in climax habitat, generally no fresh invasion takes place.

1. **HYDROSERE**—It may be studied in a pond or pool. The water is deep in the middle and gradually becomes shallow towards the edge or shore. A hydrosere present six stages in succession and these are :

(a) *Submerged stage*—In this stage, where water is more than 3.0 m in depth, only algae grow but no flowering plants develop. Some submerged angiospermic plants like *Hydrilla*, *Vallisneria*, *Potamogeton*, *Utricularia* etc. are found to grow where the water is less than 3.0 m deep—they are rooted at the bottom and form the pioneers of hydrosere.

When the water becomes shallow owing to the deposition of humus and eroded soil particles from the shore and unfit for the submerged species, then this area is occupied by new invaders.

(b) *Floating stage*—Here the water is 1.6 m in depth. Due to shallowing of water submerged plants now move into deeper water and the shallow region of the pond is now invaded by floating plants like *Lemna*, *Eichhornia*, *Ranunculus aquatilis*, *Nymphaea*, *Potamogeton* etc. These plants further constitute the pond bottom due to their death and decay—as a result water becomes too shallow and unfit for the growth of floating plants which would disappear.

(c) *Reed swamp stage*—The water now becomes 0.3—0.6 m in depth. In this stage, marshy plants like *Typha*, *Sagittaria*, *Scirpus*, *Phragmites* etc. grow—these plants are semi-submerged with their roots attached at the bottom and shoots well above the water. These plants further make the water shallow by the deposition of plant humus and other sedimentary materials, as a result water becomes unfit for the growth of plants belonging to this stage but suitable for the growth of the plants of the next stage.

(d) *Marsh meadow stage*—In this stage, the substratum changes from aquatic to marshy soil with surface water of 2.6 cm—7.6 cm only. Plants growing in reed swamp stage can not tolerate this dry habitat and therefore this habitat is invaded by *Carex*, *Juncus*, *Polygonum* and many species of Gramineae. Ultimately humus collect, meadow becomes lowland and dry—as a result plants of *marsh meadow stage* are replaced by shrubs and trees.

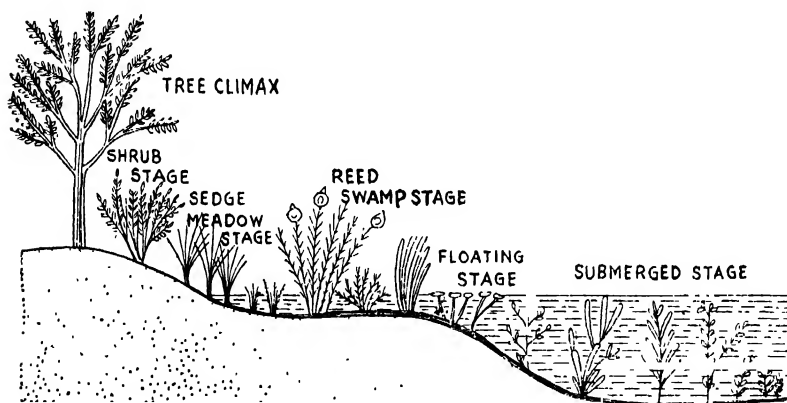


Fig. 4.2 Hydrosere—different stages in succession from a pond.
(Redrawn from Kochhar's Plant Ecology)

(e) *Woodland stage*—This stage is composed of woody shrubs and trees. Plants of this stage can tolerate partial water-logged conditions around their roots.

(f) *Climax forest*—In this stage shade-loving trees develop. The soil becomes rich in humus and micro-organisms—the air is humid and shady. This condition results in unfavourable growth for sun-loving trees—consequently shade-loving trees form the pioneer vegetation.

2. **XEROSERE**—Xerosere is initiated on bare areas like rocky lands, sand or stony lands and is characterised by extreme deficiency of

water in soil. It also shows a few stages of development e.g., (a) *crustose lichen stage* composed of crustaceous lichens, (b) *foliose lichen stage* composed of foliaceous lichens and few terrestrial algae mainly belonging to Cyanophyta group, (c) *moss stage* composed of certain xerophytic rock mosses, (d) *herbaceous stage*—in this stage xerophytic herbs colonise gradually when a thin layer of humus type of soil is formed due to decay of the bodies of lichens, algae and mosses, and also as a result of the disintegration of the surface of rocky substratum by them, (e) *shrub stage*—in this stage, xerophytic herbs are followed by xerophytic shrubs when the amount of soil increases gradually and (f) *climax forest stage*—in this stage climax type of forest formation results with the formation of reasonably thick layer of soil and humus due to decay of different plant groups in previous stages.

A. PROCESS OF SUCCESSION—In this process, migration of plants on a bare area from the neighbouring areas and aggregation on the spot of activity takes place ; then the migrants react on the soil and adjust themselves to the local climatic conditions. Thus they become pioneer plants. After getting acclimatised and balanced with the environmental conditions, pioneers begin to multiply. Subsequently interspecific and intraspecific competition for multiplying occurs. As a result of this struggle for survival and supremacy, the number of plants decreases,—further decrease in the number of pioneers takes place as they react on the environment. This changed environment becomes unsuitable for the growth and spread of the existing plants ; as a result new channels open up for the incoming of new arrivals. Pioneers, by their death and decay, increase the fertility of the soil which is suitable for the growth of new invaders. Thus community development progresses and number of new-comers at each stage decreases until the climax stage is reached when the entry of further new-comers is very difficult as the plants of the climax stage gain a good equilibrium with the environment to maintain and adjust their lives for long periods.

All types of successions, e.g. hydrosere, xerosere, halosere etc. are characterised by a similar series of stages, viz.—

- (a) *Nudation i.e.*, the formation of a bare area.
- (b) *Migration and colonisation.*
- (c) *Ecesis i.e.* the establishment and final maturation of colonising species.
- (d) *Aggregation.*
- (e) *Reaction between colonising species and habitat.*
- (f) *Competition amongst the inter- and intraspecific plants*—this is for the survival of the fittest.
- (g) *Stabilisation i.e.* the attainment of stability of dominant species after competition, and
- (h) *Climax i.e.* the final formation of species.

B. CAUSES OF SUCCESSION—In a habitat, the main cause of succession is climatic. It is the climate producing the bare area due to change in the climatic condition. As a result, initiation of a sere begins. There are also some other agencies like destruction of vegetation by fire, land-slide, flood etc. responsible for the starting of succession in vegetation. When the vegetation of a primary succession is destroyed by anyone or all of the above-mentioned factors, then secondary succession is set up. Sometimes, a succession after its development or initiation, may be deflected from its normal course by some disturbing factors like biotic agencies, fire, flood etc. Then it is called *deflected succession*. Soil condition is another cause of shaping the nature of plant community—in a seral habitat, change from one type of community to another is largely dependent on soil condition.

4.3 Methods of Studying Vegetation: Practical study of ecology of plants cannot be done solely indoors within laboratory but greater part of it depends on practical work done in the field where field investigations are carried out. The results of the observations in the field depend on keeping correct records made from such observations in a systematic manner. The practical ecological study on the vegetation of a particular region falls under two categories such as (a) initial and preliminary survey work and (b) detailed studies of particular aspects of the subject—the latter also requires experimental studies in the laboratory and analytical methods in the study of plant communities.

Survey or reconnaissance work—Survey or reconnaissance work principally consists of recording main features of plant communities of a greater area together with ecological factors operating on the said communities. This type of field work is known as primary survey and it should be done in detail and must be accompanied by photographs and vegetation maps showing the characters and distribution of plant communities of that area. Besides another important aspect in this study is the noting of biotic and other influences (i.e. activity of human and other living agencies regarding bringing about the change of plant communities) operating in that said area. The initial work in field survey involves travel in the area which is to be studied together with recording of important plant communities and their distribution concerning main habitat factors.

In the field, characteristic features of the plant communities with the member of their component species should be recorded. In the record, frequencies of different species should be indicated by suitable symbols, there should be uniformity of symbols in mapping vegetation, where mapping is usually done on 15 cm ordinance survey maps; the symbols for dominants should be included in addition to symbols used for common types of plant communities such as grassland, forests etc. Regarding recording and subsequent enlisting of the species which make up the composition of plant communities, it is usual to attach letter or letters after the names of such species to denote the frequency of occurrence in the community. The letters

indicating the degree of frequency, dominance etc. in general use for this purpose are given below :

<i>d</i> =dominant	<i>va</i> =very abundant
<i>a</i> =abundant	<i>lf</i> =locally frequent
<i>r</i> =rare	<i>f</i> =frequent
<i>o</i> =occasional	<i>-</i> =absent
<i>la</i> =locally abundant	

Of course there may be considerable discrepancy in the frequencies described by different workers, still a standard may be arrived at, in which there will be little difference. A concrete example of finding out floristic composition in a burnt out heath six years after its regeneration from burning out (biotic factor) can be made by use of such symbols—

Calluna vulgaris=*va, d*
Festuca ovina=*a*
Erica cinerea=*o*
Potentilla erecta=*o*

Another Indian example such as in a *Dipterocarpus-Mesua* forest community runs as follows :—

Dipterocarpus macrocarpus=*a*
Mesua ferrea=*a*
Litsaea khasiana=*o*

Several symbols are used in mapping vegetation to denote different types of plant communities such as savannah mixed, littoral swamp, salt marsh etc., some of which are shown as follows :—

	<p> = <i>Narenga porphyrocoma</i>—<i>a</i> ** = <i>Cymbopogon nardus</i>—<i>a</i> ↑↑ = <i>Shorea robusta</i>—<i>d</i></p>
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Sal savannah of lower
Brahmaputra valley

	<p>++ = <i>Aegicerus</i> species—<i>a</i> △△ = <i>Ceriops roxburghiana</i>—<i>vd</i></p>
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Littoral swamp

Methods of studying plant succession of a particular area consist of finding out the species, their relative abundance and distribution in that area with their spread and occurrence at different times. The following are the methods followed :—

1. *The quadrat method*—This method is adopted for studying the vegetation in general. A quadrat means any area of square, rectangular or circular of any particular spot selected for the study of vegetation. The area of the quadrat differs with the kind of vegetation e.g., low herb vegetation can be studied precisely with quadrat of 1 sq metre whereas tree or shrub vegetation study requires a quadrat measuring 100 sq metre.

Though a quadrat includes a small area of vegetation, it exhibits the exact nature of the area ; so a number of quadrats at different places of a big area reveal the entire ranges in the structure of vegetation. In order to study and analyse the vegetation in detail, quadrats should not be located at random but must be selected carefully so as to cover areas that may present all the representatives of plants there under study. So before fixing quadrats, visual reconnaissance is necessary.

Quadrats may be temporary or permanent. Permanent quadrat is fenced by wire for repeated studies and record ; temporary quadrats are used once for recording species.

2. *List or Count quadrat*—It is used for listing species and counting their numbers, it is useful in floristic study of a community.

3. *Chart quadrat*—It is used for accurate and detailed mapping to scale, the growth and distribution of species. This method is used for comparing two similar plant communities.

4. *Experimental quadrat or Denuded quadrat*—It is a permanent quadrat in which, in the beginning, all the plants are removed and the observations and recording are done on the basis of ways of re-entrance of plants there. In this quadrat, in addition to vegetation, the effect of various biotic factors and the environmental factors by installing thermometers, rain guage, thermographs, hygrographs, anemometer etc. are also studied.

5. *Transect*—It is another method of studying the vegetation which varies from the quadrat method. Transect is a continuous narrow strip of any length which gives a cross section of the vegetation. Transects are very useful in studying zones, ecotones and transitions of all types of vegetation in a community. There are two kinds of transects e.g., (a) *belt transect* and (b) *line transect*. In case of the belt transect, a strip of definite width and of length suitable for studying vegetation is marked out and plotted as in the case of quadrat, then plants occurring along the strip are recorded. In case of the line transect, a cord or measuring tape is stretched between two points and all the plants that occur on the line (i.e., along a single line) are marked out and plotted to scale. Like quadrats, transects may also be permanent or temporary. Transects also help in determining the broad relationships between plant communities and particular habitat factors in addition to the zonation of vegetation. Fixing of proper direction and length is of great importance in laying out a transect. The transect should pass across the vegetation zones and not parallel to its circumference. Determination of correct direction in the hills should be done in the spot where there is clean-cut zonal variations. A thorough reconnaissance of the area with regard to fertility gradients should also be done before fixing the direction of the transect.

Ecological Types or Classification

On the basis of the amount of water present in the soil, Warming (1909), for the first time, classified plants occurring on soil and other substrata into following *eight* groups :—

1. HYDROPHYTES—Plants that occur in water.

Hydrophytic vegetation i.e. hydrophytes are classified by various authors in different groups. Arber (1925) classified hydrophytes into (a) *rooted* and (b) *non-rooted* types. Luther (1949) classified hydrophytes into (a) *haptophytes*—plants attached only to the substrata, (b) *rhizophytes*—plants, whose basal parts penetrate the substrata and (c) *planophyta*—free floating plants with submerged or surface floating organs. Planophyta includes both microscopic *planktophytes* i.e. planktons¹ and macroscopic *pleustophytes* i.e. pleustons². Penfound (1952) divided hydrophytes into (a) *wet-land* and (b) *aquatic* forms. Aquatic form includes three types e.g., *emergent*, *floating* and *submerged*. Henny (1960) classified hydrophytes into three groups, viz. (a) *euhydrophytes*—plants with completely submerged vegetative organs, reproductive organs either submerged or aerial, (b) *hydatoaerophytes*—plants with partly submerged and partly free-floating vegetative organ, reproductive organ aerial and (c) *teuagophytes*—amphibious plants growing in substrata with fluctuating water level. Tansley (1949) and Sculthorpe (1967) classified vascular hydrophytes into two main groups e.g. (a) *rooted-hydrophytes* i.e. hydrophytes attached to the substratum and (b) *free-floating hydrophytes*. The former group is further subdivided into three types e.g. (i) *emergent hydrophytes*, (ii) *floating-leaved hydrophytes* and (iii) *submerged hydrophytes*.

According to the mode of life in aquatic environment, hydrophytes are generally divided, for convenience, into following categories :—

(a) *Free floating hydrophytes* or *free swimming* (plankton and pleuston) e.g. *Lemna*, *Pistia*, *Wolffia*, *Salvinia*, *Azolla*, members of algae etc.

(b) *Rooted submerged hydrophytes* e.g. *Hydrilla*, *Vallisneria*, *Ottelia*, *Potamogeton*, *Zostera* etc.

(c) *Rooted hydrophytes with floating leaves* e.g. *Nymphaea*, *Nelumbium*, *Limnanthemum*, *Aponogeton* etc.

(d) *Rooted and immersed hydrophytes occurring in shallow water* e.g. *Typha*, *Scirpus*, *Polygonum* etc.

The last three types are also called, according to Warming *benthos* or *fixed hydrophytes*.

2. HELOPHYTES—Plants occurring in marshy places.

In case of hydrophytes and helophytes, soil in *extremely wet* and sufficient amount of water is available for plant growth ; formations are hydrophilous.

¹ The term *plankton* is applicable for all minute, solitary colonial and unicellular or multicellular organisms. For detail refer article 5.2

² Macroscopic free-floating plant groups belonging to bryophyta, pteridophyta and spermatophyta are called pleuston or hydrocharid formations. For detail refer article 5.3

3. **MESOPHYTES** are plants which prefer a soil of moderate humidity for their growth, they are unable to grow in wet soils.

4. **OXYLOPHYTES**—These are plants growing on acid soils.

5. **HALOPHYTES**—Plants occurring on saline soils.

6. **PSYCHROPHYTES**—Plants occurring on cold soils.

Oxylophytes, halophytes and psychrophytes are growing on *physiologically dry soils*, their growth depends upon their capacity to absorb *available* water; formations are therefore composed of xerophilous species.

7. **LITHOPHYTES**—Plants occurring on rocks and stones.

8. **PSAMMOPHYTES** i.e. formations on sand and gravel.

Lithophytes and psammophytes occur in *physically dry* soils, its slight water-retaining capacity determines the vegetation. The formations are xerophilous.

Ecological types are also referred to as *habitat-forms* (Hanson and Churchill, 1965). Habitat-forms bear the impress of the habitat e.g. cacti growing in arid area, aquatic plants growing in water etc. Hence those forms are mainly ecological and are of special value as indicators of environmental conditions. According to Hanson and Churchill (1965), the habitat-forms contain three most common classes, e.g. (a) *hydrophytes* which include amphibious, floating and submerged plants, (b) *mesophytes* which include sun and shade plants and (c) *xerophytes* which include plants of dry habitats, this class may further be divided into groups on the basis of ability to endure drought.

5.1 Hydrophytes : Hydrophytes are plants growing in water or soil covered with water. Plants of lakes, ponds, streams and other aquatic environment as well as those of swamps and marshy places belong to this category. The structural adaptations of hydrophytes are correlated with decrease in oxygen supply due to slow solubility of oxygen in water, decrease or absence of structures needed for water loss during transpiration and also extreme decrease in mechanical and water conducting tissues. With regard to their relation to aquatic environment, hydrophytes are classified into (a) free floating hydrophytes, (b) rooted hydrophytes with floating leaves, (c) rooted submerged hydrophytes and (d) rooted and immersed hydrophytes occurring in shallow water or marshy land—also known as *helophytes* or amphibious plants.

A. FREE FLOATING HYDROPHYTES—They include all plants that can float freely in water; plants are not rooted in the soil. Floating hydrophytes are represented by *Pistia*, *Lemna*, *Spirodella*, *Wolffia*, *Eichhornia*, *Aldrovanda*, *Azolla*, *Salvinia* etc.—they constitute what is known as *macro* or *megaplankton* vegetation or *pleuston* formations (Warming, 1909).

Adaptations :—(1) Vegetative modes of propagation by stolons and offsets are highly developed, seeds are less developed e.g., *Eichhornia*, *Wolffia* etc.

(2) Presence of air storage tissues in stems and petioles forms a continuous air communicating system.

(3) Root system is poorly developed ; the roots when present are less branched, generally shorter and without root hairs. In some plants e.g., *Wolffia*, *Salvinia* etc., the roots are entirely absent ; the whole plant surface acts as absorbing organs. True root caps are absent, instead in some cases elongated sheath-like *root pockets* are present. The shoots in most cases (e.g. *Pistia*) have condensed short internodes.

(4) In *Lemna*, the leaves and shoots are not distinguishable ; the dorsiventral thalloid shoots function as assimilatory organs—they are all traversed by air spaces, a device for floating. Leaf lamina, being peltate, cordate and very wide assumes the shape of typical floating leaves in many cases e.g., *Lemna polyrrhiza*, *Hydrocharis* etc.

(5) The petioles are long with swollen spongy aerating tissues mostly (e.g., *Eichhornia*), in other parts too larger cavities containing air are present—those cavities give buoyancy to plants in floating.

(6) The upper surface of leaves is provided with stomata, the palisade tissue although is well developed but exceeded by spongy tissue with large air cavities.

(7) In pleuston flora, various associations may be distinguished according to dominant species e.g., *Lemna-Pistia* association, *Pistia-Wolffia* or *Eichhornia* association etc.

B. ROOTED HYDROPHYTES WITH FLOATING LEAVES—Plants in this group are rooted in the muddy soil at the bottom of ponds, lakes etc. This group is represented by species of *Nymphaea*, *Nelumbium*, *Aponogeton*, *Limnathemum* and *Victoria regia*.

Adaptations :—(1) Formation of rhizome and adventitious root system takes place.

(2) The large and rounded leaf lamina together with rhizomes, petioles, roots etc. are traversed by air cavities.

(3) The xylem and woody lignified tissues in different plant organs are poorly developed.

(4) Stomata are restricted only on the upper surface of the leaf.

(5) The epidermis of leaves is thin and almost absent—the waxy coating of the upper surface of leaves (*Nymphaea*) protects the leaves from getting wet and clogging of stomata.

(6) Air cavities in the floating leaves also form a continuous air communicating system by means of which submerged organs can exchange gases with the atmospheric air through stomata.

C. ROOTED SUBMERGED HYDROPHYTES—Plants of this group are fully submerged and are also rooted to the substratum. In India, rooted submerged hydrophytes are represented by majority of monocotyledons e.g., *Vallisneria*, *Zostera*, *Hydrilla*, *Potamogeton*, *Najas*, *Zannichellia*, *Ruppia*, *Ottelia* etc., In dicotyledons *Ceratophyllum*, some species of *Utricularia*, *Trapa bispinosa*, *Myriophyllum indicum* etc. are common. Among algae macroscopic *Chara*, *Nitella* (anchored to the substratum by rhizoids) are also common.

Adaptations :—(1) There is extreme reduction in roots and analogous organs ; some are rootless, when roots are present they are without root hairs because water and nutrient salts may be absorbed by the entire permeable plant surface under water.

(2) Leaves are much reduced in size and thickness—this is an adaptation against slow diffusion rate of dissolved gases like O_2 and CO_2 . The absorbing surface is greatly increased in linear ribbon-like much dissected leaves (in *Ceratophyllum*, leaves are dissected and narrow ; *Myriophyllum* has pinnatisect leaves)—this is due to constant water waves imparting mechanical stress. Stomata are absent. The mesophyll tissue is rarely or not at all differentiated into palisade and spongy tissues.

(3) Although, in a strict sense, transpiration is absent but excretion of water takes place by *guttation* through hydathodes.

(4) The growth of submerged plants is generally reduced – this is due to weak light intensity resulted from the formation of blooms of floating algae that may cut down light penetration.

(5) The epidermis of all the organs are not cuticled or very thinly cuticled. The xylem with associated mechanical tissues is extremely reduced as water conducting tubes are not necessary. In some cases e.g., *Najas*, xylem is represented by a solitary non-lignified cavity only. Lignification is very poor or absent, hence plants are soft and tender.

(6) Stems and other plant parts are traversed by air spaces or air cavities and often with aerenchyma (a tissue made up of thin-walled, non-suberised cells and are loosely united surrounding large air cavities). Air cavities are filled up with oxygen and carbon dioxide which are used in respiration and photosynthesis respectively by internal circulation. Sometimes air cavities are partitioned by chloroplast bearing tissue. In many cases air cavities are traversed by *diaphragms* which prevent air cavities being water logged.

(7) In some hydrophytes e.g., *Myriophyllum*, *Utricularia*, *Potamogeton* etc., common method of perennation through winter is by the formation of *winter buds* formed at their branch apices—these buds germinate into new plants with the advent of summer.

(8) In *Hydrilla*, *Vallisneria* etc. peculiar pollination is brought about in water. Female flowers with stalks remain usually submerged under water ; when mature, they come up to water level due to uncoiling of coiled stalk. In the meantime, the male flowers get detached from the stalks, float on water and are carried finally by

water current to the female flowers for pollination. After pollination female flowers sink down again in water.

D. ROOTED AND IMMERSED HYDROPHYTES OR HELOPHYTES OR AMPHIBIOUS PLANTS—These plants are adapted to grow in shallow water in which some of the parts i.e. underground parts remain under water or within water-saturated muddy soil while other aerial parts remain well above the soil surface. Thus, plants of this group are adapted to live partly in water and partly above the substratum free from water; they are also known as marsh plants or *helophytes*. Helophyte is represented by plants like *Typha*, *Scirpus*, *Sagittaria*, *Alisma* among monocots and *Ranunculus aquatilis*, *Enhydra fluctuans*, *Polygonum* spp., *Jussieuia* spp., etc. of dicots.

Adaptations :—(1) Plants are mostly perennials but during dry season annual species may prevail in dried marshy lands.

(2) Most of the plants have well developed extensive underground creeping stems (rhizomes) with profuse adventitious roots embedded in mud. Formation of tubers containing reserved food (e.g. *Sagittaria*) is another important feature.

(3) The leaves show great variation in structure. The submerged leaves are thin, sometimes much dissected and without cuticle and stomata while aerial leaves are large, entire or slightly lobed, cuticled and with stomata—occurrence of these two forms of leaf is called *heterophylly*. In case of amphibious plants, this heterophylly phenomenon is due to some physiological and ecological factors, e.g. (a) reduction of light intensity in submerged parts, (b) quantitative reduction in transpiration rate, (c) variation in hydrostatic pressure and (d) variation in growth-form and habitat etc.

(4) Anatomically, these plants are characterised by the development of mechanical and conducting tissues together with aerenchyma. Due to changes of water contents of the area, the anatomy of rhizome shows both hydrophytic and xerophytic structures, e.g. in *Typha* both mechanical and conducting tissues showing meso-xerophytic characters and aerenchyma and storage tissues showing hydrophytic characters are present.

(5) Formation of respiratory roots (pneumatophores) in some members of mangrove swamps.

(6) Germination of seeds is favoured in muddy soil having low oxygen content. Seeds and fruits are provided with air spaces and other devices that help their dispersal by water.

5.2 Plankton Formation : The term plankton was first introduced in 1887 by a German ecologist V. Hensen. According to him, the term 'plankton' indicates any dead or living organism, either plants (forming phytoplankton) or animals (forming zooplankton), that float passively in water and are easily carried about by water current or wind action.

Phytoplankton always consist of *minute* plants i.e. *microphytes*. They are either unicellular or multicellular and solitary or colonial, belonging mostly to the class algae which can manufacture their food from raw materials (i.e. autophytes), while few belong to classes fungi and bacteria living either parasitically or saprophytically.

Micro-organisms, which are free-floating throughout their entire life cycle form actually the *true plankton*. In some cases *false plankton* is formed in fresh water by the members of Chlorophyceae like *Spirogyra*, *Zygnema* etc. These plants are fixed at first stage, but due to break by constant water current and due to the expansion of gas evolved within their filaments, they rise to the surface of water and float there.

FLORA : Plankton flora belong to different lower plant groups, viz :—

(a) *Cyanophyceae*—Most of the members under this group are true phytoplankton as they are found to float a little below the surface of water but when water becomes still and undisturbed they swim in large numbers on its surface. The algae are able to ascend in water due to the presence of air containing spaces within protoplasm. Members of this group may be marine or fresh water ; they impart various colour effects on the surface of water. These colour effects are due to the presence of different types of pigments in their chromoplasm and complimentary chromatic adaptations according to environments and light intensity.

In sea and salt-water lakes there occur species of *Trichodesmium* (which colour the water red), *Nodularia* (which causes greenish-grey colour of water), *Heliothrix* (causes bluish-green colour) etc. In fresh-water ponds, lakes, jheels etc. species of *Anabaena*, *Polycystis*, *Oscillatoria*, *Gloeotrichia*, *Coelosphaerium* etc. occur.

(b) *Diatomaceae*—Members belonging to this group are generally unicellular and solitary, but may live in colony of different types ; some are also enveloped in mucilage. The common marine genera are *Thalassiosira*, *Chaetoceras*, *Rhizosolenia* etc. They impart brownish or greenish colouration to water. In fresh water, there occur species of *Fragilaria*, *Melosira*, *Cyclotella* etc.

(c) *Peridineae* (Dinoflagellata)—They are commonly found in tropical sea. Some fresh water types also occur in ponds, lakes etc. e.g. *Ceratium hirundinella*. Common marine types are represented by species of *Peridinium*, *Ceratium* etc. All are provided with flagella and are motile.

(d) *Chlorophyceae*—Many members of this group form true plankton as they are free floating and swimmers of fresh water e.g. species of *Botryococcus*, *Dictyosphaerium*, *Oocystis*, *Sphaerocystis* etc.

(e) *Schizomycetes*—This group constitutes a large section of phytoplankton. Schizomycetes are found in the ocean from the upper surface up to a depth of 1,100 meters. All are motile and mostly

of spiral type. Among Schizomycetes, nitrifying and denitrifying organisms are of great significance in relation to metabolism in water as they oxidise ammonia to nitric acid or reduce excess of nitric acid to nitrogen.

ADAPTATIONS : All plankton organisms have floating power and hence they have floating devices. Majority of them are swimmers. In some cases, they have the tendency of slow sinking. According to Klebahn (1922), pseudo-vacuoles or gas-vacuoles present in the cytoplasm of many species are floating devices against sinking ; those vacuoles make the organisms buoyant. Some organisms try to increase the *resistance form* against sinking by relative increase of their surface. According to Schutt there are several arrangements meant for surface enlargement as floating mechanism. e. g. in the form of wing-like expansions, threads, bristles, spines etc or the body itself as a whole is filiform, sometimes curved or spirally coiled as seen in many genera of diatoms and Peridinales. The watery gelatinous envelop surrounding the cell, little silicification of the valve and connecting band portion of wall preventing the organisms from becoming too heavy are perhaps other devices for floating diatomaceous planktons. Regarding types there is seasonal change in the plankton flora in a particular sea—as a result, association is changed ; this is due to change of light intensity, temperature and other environmental conditions with the season e. g. in a particular sea, in summer season, there may be plankton rich in diatoms while in the same sea, during winter, plankton flora may be rich in Peridinales.

CLASSIFICATION : Warming has classified true plankton into three sub-formations, viz :—*Haloplankton* (salt water plankton), (b) *Limnoplankton* (fresh water plankton) and (c) *Saprop plankton* (foul or brackish water plankton).

(a) *Haloplankton*—This is the plankton formation of salt water. It may be again sub-divided into *neritic* and *oceanic* types. Neritic haloplankton is confined to the coast, In tropical region, members of Cyanophyceae, Diatomaceae, Peridineae etc. constitute this type of plankton while in temperate region, Diatomaceae mainly dominate. Oceanic plankton is confined to open sea. It is chiefly composed of Peridineae, both in tropic and temperate regions.

(b) *Limnoplankton*—It forms the plankton of fresh water. In lakes, ponds etc., it may be differentiated into *neritic* near the shore and *pelagic* in the open water. Limnoplankton forms one of the most cosmopolitan type of formation and is composed of autophytic species belonging to diatoms during cold months and Cyanophyceae during summer or diatoms only throughout the year.

(c) *Saprop plankton*—It is the plankton of small pools having stagnant water which is rich in putrefying organic matter but poor in oxygen. The water become stinking and green in colour. Saprop plankton vegetation is composed of the members of Flagellata (e.g. *Euglena*), Cyanophyceae and Schizomycetes. Some members of this.

formation assimilate carbon dioxide but obtain nitrogenous compounds and other nutrients from organic constituents of water, hence they are hemi-saprophytes.

5.3 Pleuston or Hydrocharid Formation : Sometimes on the banks of stretches of fresh water, in small ponds, tanks etc., there occurs a type of vegetation of *megaphytes* which is not fixed but either free swimming or free floating like plankton—this special type of free moving megaphytic vegetation is called pleuston or hydrocharid formation. This formation is also called megaplankton or macroplankton. Pleuston formation is distinguished from genuine plankton by the following characters :—

(a) The occurrence of *different growth-forms viz., megaphytes* including mosses, water ferns (Hydropterideae) and spermatophyta,

(b) The group of algae, when present, differs from the group of algae belonging to *true plankton i. e.,* algae of pleuston actually forms *false plankton.*

FLORA : The flora consist of the following groups :—

1. Bryophyta—Both submerged and swimming species of *Riccia*.
2. Hydropterideae—*Azolla* and *Salvinia*.
3. Spermatophyta—*Hydrocharis*, *Lemna*, *Wolffia*, *Pistia*, *Eichhornia*, *Jussieuea*, *Ceratophyllum* etc.

ADAPTATIONS : See adaptations of free-floating hydrophytes (Art. 5.1, page 392).

5.4 Xerophytes : It is very difficult to ascertain an exact definition of xerophytes as the term has been explained by different ecologists in a different way from time to time. Normally xerophytes are plants of *xeric¹ i. e., dry habitats* where water supply is deficient, the soil is dry or physiologically dry² together with such atmospheric condition which promotes loss of water.

According to the above conception, all plants belonging to *oxylophytes*, *psychrophytes*, *halophytes*, *lithophytes*, *psammophytes* etc. are xerophilous *i.e.* they exhibit xerophytic characters.

According to Daubenmire (1959), “xerophytes are plants which grow on substrata that usually become depleted of growth water to a depth of at least 2 decimetre³ during a normal season”. On the basis of the above idea, Daubenmire suggests that “in arid regions all plants *not confined* to the margins of streams or lakes are considered xerophytes, whereas in regions of high rainfall the class would be

¹ Xeric is a habitat condition where the water supply is scanty and the atmospheric condition is such as greatly enhance the loss of water.

² Though soil contains much amount of water, but the water is not available to plants due to some physiological conditions of soils such as high acidity or alkalinity, less porosity of soil particles which cause the deposition of brackish stagnant water on the soil surface etc.

³ 8-10 inches.

represented only by shallow rooted plants of sandy soils.....
by algae, mosses and lichens which grow on tree bark and rock surfaces, etc.”

On earth, xerophytes have originated from mesophytes owing to the change in climate and habitat. Mesophytic plants had undergone changes as a result of increase in drought until they had become well adapted to bear extreme arid condition and habitat.

The most important feature in the adaptation of xerophytes consists (a) in the economy of available water for prevention of too much loss of water by transpiration¹ and (b) in the procurement of maximum amount of water from the lower layers of the dry soil with the help of long tap roots.

All plants showing xeromorphic² characters may not be true xerophytes. Though normally xerophytes are the inhabitants of desert regions, still they are not *strictly* confined to deserts. They can grow in all habitats where the xeric and arid conditions of the habitat and environment prevail. Their morphological and physiological metamorphosis of organs also develop in different degrees according to the degrees of habitat and environmental conditions.

Xerophytes are classified into (a) drought avoiding, (b) drought escaping, (c) drought enduring and (d) drought resisting.

(a) *Drought avoiding*—To this type belong many plants having small size with restricted growth—thus they can avoid scanty water supply.

(b) *Drought escaping*—Many annual and few biennials with very short growing and flowering season consisting of few weeks only (i.e., *ephemeral plants*) belong to this category. Plants are small in size, having large shoot system in relation to root system. During unfavourable period, their aerial parts die but underground parts remain buried in the soil from which again they develop—in this way these plants escape drought. Plants are small, dense shrubby and mostly belong to the families Boraginaceae, Compositae, Gramineae etc.

(c) *Drought enduring*—Plants under this category are true xerophytes, they are characterised by desert shrubs of heath-like habits and stunted growth. These plants can endure long and continuous dearth of water in soil. Like drought avoiding plants, drought enduring plants have little growth in a single season. Plants get wilted when moisture content of the soil decreases extremely ; their leaves fall off, but the plants continue to live. no new growth takes place until moisture is available. Drought enduring plants are mostly non-succulent perennials like species of *Acacia*, *Ephedra*, *Calotropis*

¹ In dry regions like desert, it is very difficult to obtain water by plants from the dry soil –hence this adaptation.

² Morphological and physiological characters are like that of *true* xerophytes.

procera, *Nerium odorum*, *Capparis aphylla*, *Zygophyllum* spp., *Ipomoea pes-caprae*, *Boerhavia diffusa*, *Aristida mutabilis* etc.

(d) *Drought resisting*—To this type, succulent xerophytes e.g., succulent cacti and *Euphorbia* belong. Besides, species of *Agave* and *Aloe* of Amaryllidaceae, members of Crassulaceae, Portulacaceae etc. belong to this category. These plants store up water in their succulent stems (*Opuntia* and cactus-like species of *Euphorbia*) and leaves (*Agave*, *Aloe* etc.). The stored water is used when no water is obtained from the soil. The plants continue to grow, flowering and fruiting for long periods of extreme droughts.

Characters of xerophytes are met with in the capacity of their tissues for survival during long periods of drought and dehydration. This is marked by extensive resistance against wilting.

ADAPTATIONS: Various types of morphological, anatomical and physiological adaptations are met with in xerophytes—these are:

I. Morphological:

(a) Stunted growth, scrub and cushion or succulent habits of plants—true xerophytes are mostly perennial herbs, woody shrubs, and sometimes small trees of limited growth.

(b) The leaves may be thin or rigid and leathery i.e. sclerophyllous. Extreme reduction of the leaf surface into needle-shaped structure (e.g. *Pinus*) or by their metamorphosis into spines and allied structures (e.g. cacti, succulent *Euphorbia*, *Agave* etc.) or total absence of leaves. The green stem is transformed into leaf-like cladode (*Ruscus* of Baluchistan desert).

(c) Ericoid or rolled leaves are found in many desert grasses e.g. *Psamma*—an adaptation against exposure of leaf surface in unfavourable condition.

(d) Development of long deep-seated root system with profuse branching so that roots reach long depths in search of water e.g. *Calotropis procera* of Rajasthan desert, *Calligonum comosum* etc.

II. Anatomical:

(a) Leaves and stems are covered with dense growth of hairs or covered with waxy coating. The epidermis is heavily cutinised.

(b) There is decrease in the size of guard cells—stomata are very often sunken.

(c) Formation of different types of glandular hairs, such as club-shaped, capitate etc.

(d) Presence of various types of secretory organs with various secreting substances such as calcium oxalate, calcium carbonate etc.

(e) The mesophyll tissue of leaves are provided with very small intercellular spaces and often are not differentiated into palisade and spongy tissues but only palisade-like cells are compactly arranged beneath both the epidermal layers.

(f) Development of mechanical tissue with extensive lignification, as lignified parts can withstand high temperature. In the development of mechanical tissues, bast fibres and sclerenchyma reach their maximum quantity—this condition is believed to be connected with the necessity of giving rigidity to the organs that remain in wilted condition for a long time.

(g) Presence of water storage tissue is also another marked feature of many xerophytes. Hypodermal water storage tissue occurs in many Velloziaceae—a typical xerophytic family. Mucilage is present in epidermal cells of many xerophytic plants like *Aloe*, *Ziziphus spina-christi*, *Cassia obovata* etc.

III. Physiological—

(a) Due to the maximum utilization of carbohydrates in the formation of cell wall material, the growth of xerophytic plants is slow. This is one of the reasons for the stunted growth of plants of xeric habitats.

(b) Cuticular transpiration is greatly decreased or entirely checked by heavy cutinisation of epidermis. Too much loss of water by stomatal transpiration is also checked by the formation of sunken stomata with their cavities guarded and bounded by various hairy structures, cutinized and thick-walled cells etc.

(c) The leaves of non-succulent drought resisting xerophytes have generally high osmotic pressure, by which a considerable amount of suction pressure is developed—as a result, the absorption of water from the soil is effected. The high concentration of the cell sap also prevents wilting for sometime.

(d) In xerophytic plants, generally enzyme activity is greatly affected by the water deficit condition of the tissues e.g., the activities of *amylase*, *catalase*, *peroxidase* etc. have been investigated to be higher in the tissue of xerophytes compared to mesophytes.

From the above discussion, it may be concluded that xerophytes are the plants of xeric habitats, but the exact nature of xerophytic characters of plants i.e. *xerophytism* is not clearly understood. Uptil now, it is a problematic question to decide whether xerophytes are actually xerophyllous, occurring only in deserts and dry habitats or they are simply drought resistant plants. Various ecologists have shown that desert plants grow better when grown in soil having much amount of water. In some xerophytic plants, it has also been noted that the water holding capacity of the soil is directly proportional to the amount of yield of the plants. From these conditions, Maximov (1938) concluded that “xerophytes are not always xerophyllous, at least so far as the soil moisture is concerned”. According to him xerophytes can grow better in soils having sufficient water and hence they should not be looked upon as drought resistant plants.

5.5 Halophytes : Halophytes are plants which grow and thrive in soils where some amount of soluble inorganic salts mainly sodium

chloride (NaCl) is present ; besides, magnesium chloride (MgCl_2), magnesium sulphate (MgSO_4) etc. are also present.

All halophytes are very similar to xerophytes regarding their structures and adaptations as soluble salts in soil make the soil *physiologically dry*. According to Warming, Schimper and Kearney, a halophyte is one form of xerophyte because some of the morphological and anatomical characters shown by xerophytes reappear among halophytes.

Halophytic vegetation is composed of annual and perennial herbs as well as woody species including shrubs and trees. In India, typical halophytic vegetation is represented by *mangrove formation* (refer article 5.7) of deltas and estuaries of the Ganges, the Indus, sea coasts of Orissa, Madras, Cochin, Travancore and Bombay Presidency. Besides, sea shore vegetation of any sea beach of Bengal, Orissa, Madras etc. constitutes halophytic vegetation.

ADAPTATIONS :

I. *Morphological*—

(a) Plants are smaller in height as salt solutions decrease growth in length.

(b) Leaves are *thick* and their surfaces are reduced i.e. *small*. Leaves may be semi-terate, isobilateral (*Suaeda maritima*), spathulate, oblong or scaly (*Tamarix* spp.). Sometimes coriaceous and glossy leaves also occur in trees and shrubs like *Rhizophora*, *Bruguiera*, *Nipa fruticans* etc.

(c) Stems of herbaceous plants are often prostrate as seen in members of the families Chenopodiaceae (*Suaeda*, *Atriplex* etc.), Polygonaceae (*Polygonum persicaria*) etc.

(d) Roots in many plants like *Ceriops*, *Rhizophora* (Rhizophoraceae) etc. are negatively geotropic i.e. roots come out of the soil in the form of vertical stalks called *pneumatophores*.

The problem of fixation of trees is done by prop and bow-like stilt roots (*Rhizophora*) as the soil of the tidal coasts is too soft—those roots prevent the plants from being uprooted.

II. *Anatomical*—

(a) *Succulence*—Like xerophytes, halophytes are mostly succulent. Their leaves are coriaceous, thick, fleshy and more or less translucent—these are due to abundance of cell sap, less chlorophyll content and smallness of intercellular spaces.

(b) Like xerophytes, presence of mucilage cells in the photosynthetic tissues (e.g. *Sonneratia* spp. of the family Sonneratiaceae, *Aegiceras majus* of the Family Myrsinaceae). The nerve ends in the leaves dilate into water storage tracheids.

Various organs of leaves of mangrove plants have been interpreted by Maximov as *hydathodes*.

(c) In many plants like *Rhizophora*, *Aegiceras*, *Sonneratia* etc. idioblasts in the form of stone cells also occur in the palisade tissue.

(d) In halophytes, palisade tissue is massive, intercellular spaces are small and often absent. Palisade tissue is mainly chlorenchymatous. Stomata are either *sunken* or lie at or near the level of the epidermis, outer walls of epidermal cells are *heavily cuticularised* and *thick*.

(e) Plants are coated with *wax* which causes the glaucous and mat surface of plants. Some plants are provided with *hairy coating* (in case of sand halophytes).

(f) *Lignification*—Lignification of woody tissues is extremely poor ; in this respect only, halophytes deviate from true xerophytes.

III. Physiological—

(a) *Respiration*—The problem of respiration is a matter of difficulty in the soil which is saline, water-logged and rich in putrefying organic bodies—hence poor in oxygen. This problem is solved in many plants like *Rhizophora*, *Avicennia*, *Ceriops* etc. by negatively geotropic root known as *pneumatophores*, which stand vertically above saline water or mud. These roots are provided with pores which are in direct communication with outer atmosphere and tissues inside. Sometimes prop roots of *Rhizophora* serve as respiratory roots.

(c) *Germination of seeds*—The seeds can not germinate in such saline soil which is deficient in oxygen. Hence species of *Rhizophora*, *Ceriops*, *Bruguiera* etc. show vivipary i.e., the development and growth of embryo in the seed when the fruit is still attached to the plant. This adaptation is a precaution against the failure of germination of seeds in saline soil. The embryo grows out of the seed and finally out of the fruit with the display of long hypocotyl and radicle, in such condition the seed with developed embryo gets detached from the plant and falls on the soft muddy soil, as a result the radicle of the embryo gets embedded in the soil.

(c) *Transpiration problem and water supply*—Regarding these factors halophytes show xerophytic characters because the soil is physiologically dry. Saline water can not be absorbed profusely as it is injurious to cells. Due to scarcity of available water, transpiration is prevented by the various kinds of morphological and anatomical modifications of leaves.

5.6 Mangrove vegetation : Champion has classified mangrove vegetation into two forest types, e.g. (a) *beach forests* and (b) *tidal forest* i.e. *typical* or *true mangrove swamp vegetation*.¹

A. BEACH FORESTS OR SANDY SEA SHORE VEGETATION—In India beach forests occur in Madras, Travancore, Bombay, Orissa and West Bengal sea coasts. The beach soil is mainly sandy and little saline with adequate lime formed from shell fragments ; water level is low

and the temperature is moderate. The annual rain fall varies from 1000-1400mm.

In sandy sea beach, four types of associations are met with viz. :—
(i) *Casuarina* association, (ii) *Pes-caprae* association, (iii) *Canavalia* association and (iv) *Spinifex* association.

(i) *Casuarina* association—In this association, *Casuarina equisetifolia* (Casuarinaceae) forms the dominant species forming characteristic fringe forest along with other deciduous species.

(ii) *Pes-caprae* association—In sandy sea shores of Digha (Midnapur, West Bengal) and Orissa, *Ipomoea pes-caprae* (Convolvulaceae) forms the predominant vegetation. The stem is creeping and very long, roots are branched and extend for a long distance, forming a net work of close-set vegetation on sand; leaves are bilobed and fleshy. It binds sand with the help of its long branched roots coming out from nodes. *Ipomoea pes-caprae* has typical xerophytic aspects and endures temperature of the hot sand. In Orissa sea beach, another sand binding species e.g. *Geniosporum prostratum* belonging to the family Labiatae also occurs.

(iii) *Canavalia* association—This association is represented by *Canavalia lineata* (Papilionaceae) together with *Fimbristylis sericea* (Cyperaceae), *Suaeda nudiflora* (Chenopodiaceae) etc. The structure and physiognomy are like those of xerophytes; root are profusely branched, leaves are sometimes thick, fleshy and with water storage cells.

(iv) *Spinifex* association—The most important and commonly occurring scrubby grass of India sea shore is *Spinifex littoreus* (Gramineae). Like *Ipomoea pes-caprae*, it also binds sands of sea-shore. *S. littoreus* possesses underground rhizome and has large development of water storage tissue. Adventitious roots are profusely branched, leaves are more or less thick. Spikelets are in spherical head-like clusters rolling before the wind over the sand and scatter the seeds like steppe plants. *Spinifex* association is dominated by *Spinifex* species and thus forms a pure association, rarely *Ipomoea pes-caprae* accompanies this association.

Other plants occurring along with above mentioned association on sandy beach are *Eragrostis reparia* (Gramineae), *Euphorbia thymifolia*, *E. pilulifera* (Euphorbiaceae), *Sida* species (Malvaceae) etc. All these species are small-leaved and more or less fleshy. Indian sandy sea shores are dominated by creeping perennial herbs whose prostrate shoots spread loosely over the sand on all sides, many of them with or without striking roots.

The sand flora of sea shore represent typical xeric characters to some extent; for this it is very difficult sometimes, to distinguish between true halophytic vegetation of sea shore and xerophytic vegetation of dry, warm, non-saline sand (as seen in Digha) which borders on the shore or occurs in inland dunes. There is another

association, commonly met with in Digha sea shore, which is *Pandanus* association mainly composed of *P. tectorius* (Pandanaeeae).

Sandy sea shore vegetation is frequently succeeded on the landward side by forest and bushland, which may also appear inland on saline sand. Warming regards these vegetations as *halophilous*, as they occur only on sea coasts and their roots extend down to saline water permanently. The following associations are commonly met with :—

(1) *Barringtonia* association—This association is mainly dominated by large-leaved and large-flowered *Barringtonia* species (Myrtaceae), other species like *Hibiscus tiliaceus*, *Thespesia populnea* (Malvaceae), *Casuarina equisetifolia* (Casuarinaceae), *Heritiera littoralis* (Sterculiaceae) also occur. This association is chiefly found in eastern Asiatic and Australian halophilous forests.

(2) *Coccoloba* association—This is found in West Indian sea coasts, mainly dominated by *Coccoloba uvifera* (Polygonaceae) in the form of small tree or shrub with large rigid leaves.

(3) *Restinga* association—This is the characteristic formation of Brazil coasts. Cactaceae and Bromeliaceae play a prominent part.

(4) *Aphyllous halophytic forest*—This is seen in the sea shores of central Asia, and dominated by a tree *Haloxylon ammodendron* (Chenopodiaceae).

(5) *Tamarisk bushland*—It is seen in Asia and Mediterranean countries. Tamarisk bush land presents a dull bluish appearance.

B. THE TRUE MANGROVE, THE TIDAL FOREST OR LITTORAL SWAMP FOREST—This type of forest comes under the category *helophilous* of the division halophytes (Warming). Helophilous plants grow on swampy, saline and clayey substratum. Mangrove swamp is the best known among all plant communities confined to swamps in salt or brackish water. It occurs in all tropical seas, mainly on muddy and flat shores where water is calm as in estuaries, deltas, lagoons etc. Sometimes mangrove vegetation extends far inland along the banks of river. The soil is either permanently flooded with water or at the time of high tide. In general, mangrove vegetation assumes the form of bushland and when viewed from the sea it appears as a dark green and dense mass of low trees with numerous aerial arched roots.

Typical i.e. true mangrove vegetation does not occur in open beach or in sandy or rocky shores of the sea. The vegetation is best developed in the wet tropics where the tropical rain forest is the climax vegetation. They extend to about 32° latitudes of both sides of the equator. There are two distinctly marked mangrove formations in the world e. g. (a) the *eastern mangrove*, found on the coasts of Indian ocean and the western part of the Pacific ocean and (b) *western mangrove*, found on the coasts of North and South America, the West Indies and West Africa.

Plants composing a mangrove formation are relatively poor in the number of species, but they all show some similarity in their general shape, size and in their physiological adaptations. Most of the species are *gregarious* in habit. Typical mangrove species have usually *pneumatophores* or *breathing roots*, *viviparous seeds* and some *special mechanism* or means in the fruits and seeds for dispersal by water currents. In addition to typical mangrove plants there are a number of associated species termed "*semi-mangrove*" by Tansley and Fritsch (1905). The common palm *Nipa fruticans* (Palmae) which forms extensive communities in saline areas belongs to "*semi-mangrove*" group.

The general distribution of the World's mangrove species is as follows—

Families	Species in eastern Mangrove	Species in western Mangrove
1. Rhizophoraceae	1. <i>Rhizophora mucronata</i> 2. <i>R. candelaria</i> (= <i>R. conjugata</i>) 3. <i>Ceriops tagal</i> (= <i>C. candolleana</i>) 4. <i>C. roxburghiana</i> 5. <i>Bruguiera cylindrica</i> (= <i>B. caryophylloides</i>) 6. <i>B. eriopetala</i> 7. <i>B. gymnorhiza</i> 8. <i>B. parviflora</i> 9. <i>Kandelia candel</i> (= <i>K. rheedii</i>)	1. <i>Rhizophora mangle</i>
2. Combretaceae	1. <i>Lumnitzera coccinea</i> 2. <i>L. racemosa</i>	1. <i>L. racemosa</i>
3. Sonneratiaceae	1. <i>Sonneratia acida</i> 2. <i>S. alba</i> 3. <i>S. apetala</i> 4. <i>S. caseolaris</i>	
4. Rubiaceae	1. <i>Scyphiphora hydrophyllacea</i>	
5. Myrsinaceae	1. <i>Aegiceras majus</i>	
6. Acanthaceae	1. <i>Acanthus ilicifolius</i>	
7. Meliaceae	1. <i>Xylocarpus moluccensis</i> 2. <i>X. granatum</i> (= <i>X. obovata</i>) 3. <i>X. gangeticum</i>	
8. Verbenaceae	1. <i>Avicennia officinalis</i> 2. <i>A. marina</i> 3. <i>A. lanata</i> 4. <i>A. lanata</i> var. <i>alba</i> 5. <i>A. eucalyptifolia</i> 6. <i>A. balanophora</i> (Australia only)	1. <i>Avicennia nitida</i> 2. <i>A. tomentosa</i>
9. Palmae	1. <i>Nipa fruticans</i>	

From the above list, it is evident that eastern mangrove contains maximum i.e. about 28 species while western mangrove has only 4 species. An analysis of the distribution of mangrove species by

Chatterjee (1957) shows that there are 23 species in South East Asia ; of these 18 occurring in India, 10 in Australia, 9 in Madagascar, 8 in East Africa, 4 in eastern America, 3 in West Africa and 2 in western America. Watson (1928), for the Malayan coastal mangrove, has shown that distribution of species within a mangrove area follows a zonation parallel to the shore line. According to him there are five zonations from the sea water to inland, these are :—(a) *Avicennia-Sonneratia* type, (b) the *Bruguiera caryophylloides* type, (c) the *Rhizophora* type, (d) *Bruguiera parviflora* type and (e) the *Bruguiera gymnorrhiza* type. From this it is evident that the innermost zone contains *Bruguiera gymnorrhiza* which is the final stage of the development of mangrove forest.

5.7 Mangrove Forests of India : Bordering the Indian ocean and its vicinity, the most important type areas are found in the Sunderbans in the estuary of the Ganges, Brahmaputra system, the Andaman Islands and the Irrawady delta. Small remnants of mangroves are also found in the estuaries of the Mahanadi, the Godavari and the Krishna on the east coast. The west coast mangroves can be divided into two forms viz. the open scrubby mangroves of the Kutch and Saurashtra coasts and the close forests extending from the mouth of the Narmada and Tapti southwards in the Mysore and Kerala States. Champion considers the tidal forest to be a primary seral type of the moist tropical forests. According to him mangrove forests may be distinguished into following types :

(a) *Low mangrove forests*—Forests of this type are very dense and composed of mainly low trees and large shrubs on an average 3-6 m in height. Few species are gregarious and evergreen with coriaceous leaves. This type is found mainly in Sunderbans ; the dominant species are *Ceriops roxburghiana* and *Avicennia officinalis* ; *Rhizophora* is absent.

(b) *Tree mangrove forests* are found mainly in Irrawady delta, also sometimes in Sunderbans. The forest soil is covered with saline water and where it is not covered with water at low tide, the soil is soft, deep black mud, full of rotting organic bodies with bacteria. Dominant species are *Rhizophora mucronata* and *Sonneratia apetala*. The *Rhizophora* and *Sonneratia* form the lowest outermost fringe and the type is stable over long periods but gradually changes into *Heritiera* as the level rises. This type is also found over 82 square miles in the Andamans.

(c) *Salt water Heritiera forests*, found typically in Irrawady delta—the characteristic species are *Heritiera fomes*, *Bruguiera gymnorrhiza*, *Excoecaria agallocha* etc. ; growth of species upto 18 m in height.

(d) *Fresh water Heritiera forests*, found in Irrawady delta and Sunderbans—characterised by extensive growth of *Bruguiera* and *Heritiera* upto 30.5 m.

Khan (1957) in his ecological studies of the mangrove forests

in India has divided the zone of the occurrence of mangrove forests of India into following regions—

I. *West-Coast of the Indian Peninsula—*

- (a) Coast line of Saurashtra and Kutch.
- (b) Coast line of Bombay State from the mouth of the Narmada Southwards.
- (c) Coast line of the states of Mysore and Kerala.

II. *East-Coast of the Indian Peninsula—*

- (d) Coast line of the State of Madras.
- (e) Coast line of the Andhra Pradesh and Orissa.
 - (i) The Cavery System.
 - (ii) The Krishna System.
 - (iii) The Godavari System.
 - (iv) The Mahanadi System.
- (f) The Sunderbans of the State of West Bengal.

III. *The Andaman and the Nicobar islands—*

I. A. THE COAST LINE OF SAURASHTRA AND KUTCH—The coast of Kutch in some places (*i e.*, from the sea in the South and West and from the Rann in the North and East) is slightly raised and fringed with mangrove swamps. The coastal vegetation from sea inwards is as follows :

On sea coast—*Avicennia officinalis* associated with *Aegiceras majus* and sometimes with *Pandanus tectorius*.

On salt marshes along the coast—*Bruguiera gymnorhiza* together with *Aeluropus villosus* grass.

In salt marshes and tidal creeks—*Rhizophora mucronata* and *R. conjugata*.

B. THE COAST LINE OF BOMBAY STATE FROM THE MOUTH OF THE NARMADA SOUTHWARDS—Mangrove vegetation of this region is divided into following zones :

(a) Coastal sea water and semi-fluid mud—Common species occurring in this area are *Avicennia officinalis*, *Acanthus ilicifolius*, *Rhizophora mucronata*.

(b) Salt marshes along the coast—*Aegiceras majus*, *Acanthus ilicifolius*, *Carapa obovata*, *Bruguiera gymnorhiza*, *Ceriops candolleana* etc. are found.

Salt marshes of tidal creeks—*Rhizophora mucronata*, *R. conjugata*, *Sonneratia apetala*, *S. acida*, *Excoecaria agallocha*, *Lumnitzera racemosa* etc.

(c) Interior drier marshes—*Clerodendron inerme*, *Aeluropus repens*, *Suaeda fruticosa* etc.

C. COAST LINE OF THE STATES OF MYSORE AND KERALA, and

II-D. COAST LINE OF THE STATE OF MADRAS (EAST COAST)—The mangrove forests of these two regions also have been divided into three zones. The coastal sea water and semi-fluid mud zone of both contain *Rhizophora mucronata*, *R. conjugata*, *Kandelia rheedii*, *Bruguiera gymnorhiza*, *B. caryophylloides*, *Acanthus ilicifolius* etc. Only the West coasts of Mysore and Kerala contain *Ceriops candolleana* and *Bruguiera eriopetala*.

Salt marsh zone along the coast is dominated by *Lumnitzera racemosa*, *Excoecaria agallocha* and *Arthrocnemum indicum*. East coast of Madras is more rich having species of *Avicennia*, *Salicornia*, *Scyphiphora* etc. In the salt marshes of tidal cracks *Aegiceras majus* and *Heritiera littoralis* occur dominantly in addition to *Sonneratia apetala*, *Avicennia officinalis* (in West coast of Mysore and Kerala only). Towards the interior dry marshy lands of East coast of Madras, only *Suaeda nudiflora*, *S. maritima*, *S. monoica* occur.

E. THE COAST LINE OF THE STATES OF ANDHRA PRADESH AND ORISSA :

(i) *The Cavery System*—This area contains poor type of mangrove forest which is interspersed with blanks. Following species are found in the tidal forests :

Avicennia officinalis, *Acanthus ilicifolius*, *Aegiceras majus*, *Clerodendron inerme*, *Excoecaria agallocha*, *Suaeda nudiflora* etc. Bush of *Rhizophora mucronata* is also noted. In dry evergreen forest, following species are mainly found—*Memecylon edule*, *Salvadora persica*, *Maba buxifolia*, *Mimosops littoralis*, *M. elangi* etc.

(ii) *The Krishna System*—In this region the species occurring on the tidal mud of sea-face are—*Rhizophora mucronata*, *R. conjugata*, *Ceriops roxburghiana*, *Bruguiera conjugata*, *Sonneratia apetala* and *Acanthus ilicifolius*. The tidal marshes near the coast bear *Lumnitzera racemosa*, *Scyphiphora hydrophyllacea*, *Avicennia marina*, *Excoecaria agallocha* and *Arthrocnemum indicum*. The inner drier salt marshes contain *Suaeda nudiflora* and *S. monoica*.

(iii) *The Godavari System*—This region is composed of typical mangrove species of *Rhizophora*, *Bruguiera*, *Sonneratia*, *Acanthus* etc. Mangrove forests of Godavari system can be divided into (a) *naked mud flats* where no vegetation appears until the elevation reaches the high tide level, (b) *pure crop of Avicennia marina* and *A. alba* together with *Acanthus ilicifolius* as an association, (c) *mixed Avicennia forest*, this forest is associated with *Sonneratia apetala*, *Rhizophora mucronata*, *R. conjugata*, *Bruguiera gymnorhiza*, *B. caryophylloides*, *Ceriops roxburghiana*, *Acanthus ilicifolius*, *Clerodendron inerme*, *Dalbergia spinosa*, *Derris aliginosa* etc., (d) *Excoecaria agallocha* and *Lumnitzera racemosa* forest with blanks—other species occurring in this forest are *Aegiceras majus*, *Thespesia populnea* and *Tamarix gallica*, (e) *extensive blanks with Suaeda maritima* and (f) *grassy blanks* suitable for paddy cultivation.

(iv) *The Mahanadi System*—The littoral forest vegetation of the Mahanadi delta is divided¹ into (a) tree covered forest and (b) open forest. The 'tree covered forest' is again divided into (1) *deltaic swamp forest* and (2) *littoral scrub jungle*. Open forest is divided into (i) sands, (ii) rocky faces near the sea and (iii) saline marshes. The mangrove vegetation is confined only to deltaic swamp forest and saline marshes. Deltaic swamp forest is mainly composed of *Rhizophora mucronata* which is associated with *R. conjugata* (less common), *Ceriops roxburghiana*, *Kandelia rheedii*, *Bruguiera gymnorrhiza*, *B. eriopetala*, *Sonneratia apetala*, *Lumnitzera racemosa*, *Heritiera fomes*, *Thespesia populnea*, *Excoecaria agallocha*, *Brownlowia lanceolata*, *Carapa obovata*, *Dalbergia spinosa*, *Derris uliginosa*, *Salvadora persica*, *Tylophora asthmatica*, *Pandanus tectorius*, *Phoenix paludosa*, *Acanthus ilicifolius*, *Premna integrifolia*, *Clerodendron inerme*, *Flagellaria indica* etc. The saline shores also contain the same species but are dominated by *Acanthus ilicifolius*, *Salicornia brachiata*, *Suaeda monoica*, *S. nudiflora* etc.

F. THE SUNDERBANS OF THE STATE OF WEST BENGAL—Sunderbans are large forest tracts located in the Gangetic delta on the southern parts of West Bengal and Bangladesh between the Hooghly river on the West and the Meghna of Bangladesh in the East. The forest tracts of Sunderbans comprise low lying swampy islands formed by main tributaries of the Ganges, the whole area is occupied by extensive forests and the vegetations are principally of mangrove types.

Prain (1903) has divided the Sunderbans into three parts, viz. (a) southern coastal strip and south-western part containing mainly mangrove species, (b) the central zone of *Heritiera* and (c) the north-eastern part of Savannah type vegetation.

The muddy flats are colonised by *Rhizophora* species, together with the association of *Arthrocnemum* and *Salicornia*. Slopes covered with fresh water during rainy season bear a luxuriant crop of *Oryza coarctata*. Marshy saline slopes are covered by *Avicennia alba* and *Acanthus ilicifolius*.

Distribution of species, as influenced by the sea, on the banks of rivers and channels of Sunderbans is as follows :

1. Fresh mud banks of rivers—*Sonneratia apetala*.
2. Banks of large rivers—*Rhizophora* spp., *Kandelia rheedii*, *Ceriops* spp., *Bruguiera gymnorrhiza*.
3. Banks of smaller channels—*Sonneratia acida*, *Avicennia alba*, *Carapa obovata*, *Aegiceras majus*, *Cerbera odollum*, *Kandelia rheedii*, *Pongamia* spp., *Hibiscus tiliaceus*, *Dalbergia spinosa*, *Ceriops roxburghiana*, species of *Lumnitzera*, *Premna*, *Clerodendron*, *Phoenix*, *Barringtonia*, *Dolichandrone rheedii* etc. Climbers are many.
4. Banks of narrow channels—*Aegiceras majus* and *Brownlowia* spp.

¹ Haines, H. H. 1925. *Bot. of B. & O.*

5. Banks of narrowest channels—*Nipa fruticans*.

The central zone is the *Heritiera* forest. *Heritiera fomes* is associated with *Acanthus ilicifolius* and *Pandanus*. On higher grounds *Heritiera* is associated with *Avicennia officinalis*, *Excoecaria agallocha* and *Cynometra* spp., while in swampy area it is associated with *Carapa gangetica* and *Amoora cucullata*. *Excoecaria agallocha* forms a transitional association between mangrove and *Heritiera* forests.

Curtis (1933) has divided Sunderbans into three regions viz, (a) the fresh water forests composed of *Sonneratia apetala*, *Avicennia officinalis*, *Acanthus ilicifolius*, *Excoecaria agallocha*, *Ceriops roxburghiana*, *Carapa obovata*, *C. moluccensis*, *Aegialitis rotundifolia*, *Rhizophora conjugata*, *Kandelia rheedii*, *Bruguiera gymnorhiza*; (b) moderately salt water forests consisting of the same species of *Excoecaria*, *Kandelia*, *Ceriops*, *Carapa*, *Bruguiera*, *Avicennia*, *Sonneratia*, *Aegiceras majus*, *Nipa fruticans*, *Lumnitzera racemosa*, *Heritiera fomes* (in clumps) and (c) salt water forests mainly composed of the above mentioned species of *Heritiera*, *Ceriops*, *Excoecaria*, *Bruguiera* etc.

Besides above mentioned plants, Sunderban flora of W. Bengal and Bangladesh is represented by many climbers belonging to families Asclepiadaceae and Leguminosae. To Asclepiadaceae belong *Sarcolobus globosus*, *Dischidia nummularia*, *Hoya parasitica*, *Finlaysomia obovata* etc. Leguminous climbers are represented by *Derris sinuata*, *D. uliginosa*, *Dalbergia candenatensis*, *Mucuna gigantea*, *Cynometra ramiflora* etc.

The savannah of Sunderbans is mainly composed of *Phragmites karaka*, *Cyperus exaltatus*, *Scirpus grossus*, *Cladium riparium*, *Saccharum spontaneum*, *Andropogon intermedius*, *Imperata arundinacea* and *Myriostachya wightiana*. Orchids are represented by *Cirrhopetalum roxburghii* (endemic species), *Oberonia gammiei*, *Acampe dentata* and *A. longifolium*. Common ferns are *Drymoglossum piloselloides*, *Acrostichum aureum* etc.

In addition to typical mangrove species, many other common species belonging to different families are also occurring, these are :

Aegle marmelos (Rutaceae), *Cassia fistula* (Caesalpinaceae), *Acacia arabica* (Mimosae), *Vitex negundo* (Verbenaceae), *Ixora parviflora* (Rubiaceae), *Pongamia glabra* (Papilionaceae), *Barringtonia acutangula* (Lecythidaceae), *Trewia nudiflora* (Euphorbiaceae), *Calamus rotung* (Palmae) etc.

III. THE ANDAMAN AND THE NICOBAR ISLANDS—The Andaman and the Nicobars have nearly 450 and 13.8 square miles of mangrove forests, this forest develops in areas covered by brackish water at high tide such as mud-flats along tidal streams. Here the forests are of gregarious type i.e. they are largely composed of single species or a few allied species. The dominant family being Rhizophoraceae which grow typically on the outer seaward fringe of the swamp where the water is mostly salty.

The mangrove vegetation of the Andaman and the Nicobar islands in different zonations, as described by Chenagapa (1944)¹ and Sahani (1957),² consists of following species :

Zonations	Species
1. Fringing the open sea	<i>Rhizophora mucronata</i> , <i>R. conjugata</i> .
2. In tidal creeks	<i>Bruguiera gymnorhiza</i> , <i>B. parviflora</i>
3. Tidal swamps	<i>Avicennia officinalis</i> , sometimes mixed with <i>Ceriops candolleana</i> , <i>Kandelia rheedii</i> , <i>Carapa obovata</i> , <i>C. moluccensis</i> , <i>Sonneratia acida</i> , <i>S. alba</i> , <i>Acanthus ilicifolius</i> , <i>Excoecaria agallocha</i> , <i>Cerbera odollum</i> .

ADAPTATIONS :

(1) *Fixation*—See under halophytes, page 402

(2) *Respiratory roots*—See under halophytes, page 403

(3) *Germination and vivipary*—See under halophytes, page 403

(4) *Means of migration*—All littoral plants are widely distributed. It has been noted that mangrove flora includes more or less the same species along all the tropical shores from Australia to East Africa—this is due to efficient means of dispersal which is done by fruits, seeds and seedlings that can float for a very long time ; all such organs are provided with *air spaces* and have *less specific gravity*.

(5) *Xerophytic structures*—See under halophytes, page (402) (anatomical adaptations).

ECONOMIC IMPORTANCE OF MANGROVE PLANTS—Mangrove plants play an important role in the following aspects—

(a) Fire wood, timber and farming materials from the bark are obtained from many mangrove plants.

(b) By obstructing the direction of water current, mangrove plants help in the deposition of silt ; they also help in soil conservation by binding the soil with their tangled mass of roots.

(c) Indirectly, they help in land reclamation by the gradual rise of the ground level and consequent spreading of the mangrove forest further to the sea.

5.8 Lithophytes : Lithophytes include plants that grow on rocks or stones. According to Warming, vegetation on *true rocks* only comes under lithophytes, but not the vegetation on the loose soil covering rock. Nature of rock i.e., its hardness, specific heat, tendency to split etc. play an important role in the determination of

¹ Chenagapa, B. S. 1944. Andaman Forests and their Regeneration. *Ind. For.* 70 (9-11).

² Sahani, K. C. 1957. Mangrove Forests in Andaman and Nicobar Islands. *Proc. Mangrove Symposium*. Calcutta.

vegetation, Sometimes rocks are *bare*, vertical, completely *dry*, bathed in burning sunlight without any cracks ; again rocks may be in shady gully and cracked where water slowly trickles. On the basis of these conditions of rocks, Schimper has classified vegetation on rocks into two formations viz., (a) *lithophytes* where the *vegetation is strictly forming on the bare surface of rocks or stones* and (b) *chasmophytes* where the *vegetation is more copious and forming on cracks, fissures and crevices of rocks* in which the components are finely grained and more water accumulates than on the bare surface.

A. LITHOPHYTES—Lithophytes include plants that can grow and colonize on steeply inclined and bare rock. The flora is chiefly cryptogamic which include algae, lichens and mosses. Of these, algae and lichens are the first dominant colonists, they belong to growth-forms that are capable of absorbing water derived from rain, dew, melting of snow through their entire surface.

Algae may give the colour to vertical rocks, e.g., *Trentepohlia* (Chlorophyceae) imparts reddish and yellowish hue to the rocks of Darjeeling and other area. Members of Cyanophyceae predominate in some tropical rocks where abundance of moisture and high temperature prevails, *Stigonema* (Cyanophyceae) imparts black stripes running down the rocks of some hills and indicates thereby the type of algal vegetation. In most cases, algae fix themselves on rocks by the aid of a mucilaginous layer of cell wall.

The lichens include both crustaceous e.g., *Lecanora*, *Lecidea*, *Biatora* etc. and foliose type e.g., *Parmelia*, *Xanthoria*, *Gyrophora* etc. The mosses include species of *Hypnum*, some greyish species of *Grimmia* and the blackish-brown members of *Andreaea*—all these form dense cushions on rock over which their filamentous protonema spread as flat incrustations.

ADAPTATIONS : As the substratum on which lithophytes grow is *extremely physically dry* (because water cannot be retained by hard non-porous steep rocks), so the lithophytes are capable of absorbing water derived from rain, dew, melting snow or water running down the rocks through their entire surface. Various devices for absorbing such water are possessed by mosses in the form of *felted rhizoids* and by some liverworts in the form of special *concave leaves*.

In many lithophytes, special attaching organs e.g. *haptera* are developed. By the help of *haptera*, they can attach themselves to the rocks.

For mineral nutrients, lithophytes are mainly dependent on atmospheric precipitations and on dust conveyed to them by wind ; although to some plants (e.g. lichens) rock is a nutritive substratum into which they penetrate more or less deeply.

Lithophytes have the capacity to endure long *desiccation* which is due to the surface rocks becoming very hot as exposed to rays of sun or due to cold, dry wind etc.

Ecologically, lithophytes are closely related to epiphytes and are often identical with them.

Associations : Though lithophytes form low organised plants, still they display great differences in their ecological demands. Different formations and associations of them can be established in relation to the condition prevailing on rocks. The following ecological conditions are concerned with them :

(a) Nature of rock, (b) degree of exposure to heat, light, moisture, wind action etc., (c) steepness of the rock surface, (d) supply of flowing water and (e) geographical situation and altitude. It has been shown that different species of lichens show varying resistance to the action of winds.

Among lithophytes there is competition and struggle for space ; due to this, various associations of lichens have been recognised e.g. *Lecanora* association on exposed boulders, *Lecanora-Calcareo-Contorta* association on horizontal limestone surfaces etc. On the surface of bare rock, the first colonists viz. algae and crustaceous lichens gradually produce a nutritive substratum upon which more highly organised species like fruticose lichens and mosses grow later—the former i.e. first colonists have horizontally extended vegetative organs and are appressed to the rock, their immediate successors i.e. second colonists rise above their surface as cushions or miniature shrubs (as found in *Cladonia* species).

B. CHASMOPHYTES—Chasmophytes are plants rooted in fissures or clefts and crevices of rocks which are filled with earth, dust and other gravel or rock-debris. In the fissures and crevices of rocks, particles of earth conveyed by wind and water accumulate. The amount and rate of accumulation depend upon the width and situation of those crevices and fissures. Thus, in the soil of fissures and crevices constituted plants settle, their dead fragments further supply the nutritive material in the fissures. Chasmophytic flora consist of all types, they belong to Thallophyta, Bryophyta, Pteridophyta and Spermatophyta. The flora varies with some prevailing factors like exposure, width and position of clefts or fissures and also according to some authors, with the presence or absence of any snow cover at the time of winter. The same rock may produce lithophytic or chasmophytic vegetation ; when rock is very steep and devoid of clefts or crevices, only lithophytes develop upon it and the rock is practically bare of vegetation. On the other hand, if the rock is provided with clefts and crevices, only chasmophytes develop in these.

ADAPTATIONS : Rhizoids and roots are often constricted within narrow clefts and flattened out as thin filamentous structures. Both tap and adventitious roots are flattened filling the cleft.

The constituent species are normally tufted in growth and do not spread far from the general root system.

In case of creeping perennial species (e.g. *Fragaria*), vegetative method of reproduction takes place with the help of long thin

epigeous runners ; these runners give rise to new shoots either in another cleft or in the same cleft in which the parent plant is established.

Rosette plants are common—this habit is, of course, the characteristic of plants freely exposed to light.

Both succulent and non-succulent *xerophytes* are common, these are represented by the families Crassulaceae, Saxifragaceae, Orchidaceae etc. Plants are provided with either small, thick and imbricate leaves or small, dry and leathery leaves.

5.9 Mesophytes : Mesophytes are plants growing in habitats that are neither too dry nor too wet. Plants under this class show a preference for soil and air of moderate humidity ; they avoid soil containing much amount of salts or soil covered with standing water. The soil in which mesophytes grow is rich in alkaline humus ; the solutes are not too dilute nor too concentrated, the oxygen supply to roots is moderate.

Though mesophytic communities occur in very diverse climates, yet they are not exposed to the danger of continuous drought. All cultivated and common land plants i.e. terrestrial plants growing around us are examples of mesophytes. Mesophytes are of two kinds according to the intensity of light to which they are exposed viz. the sun and shade plants (refer art. 3.1, (d) page 370 for detailed discussion). Mesophytes show intermediate features between xerophytes and hydrophytes regarding morphological characters. So they exhibit characters of dry land plants on one hand and amphibious plants on the other. It is found that both hydrophytes and xerophytes are changed to mesophytes due to permanent change of environment.

Adaptations :

(1) The roots are extensive and branched but of moderate length ; the diameter of the root is more or less equal to the aerial parts.

(2) Vegetative organs are devoid of hairy or waxy coatings, they are mostly fresh green.

(3) The leaves are well developed, usually dorsiventral in structure and large, more varied in form than in xerophytes ; teeth and other incisions are common. Hydathodes seem to be frequent. Leaves are green due to abundant chloroplasts in the mesophyll tissue.

(4) The stomata are numerous and present on the lower epidermis of leaves ; guard cells have maximum capacity for adjustment and controlling transpiration, aqueous tissue formation is very poor or not at all developed.

(5) The most remarkable feature of the mesophytes consists in the differences between persistent and deciduous nature of leaves. In mesophytes which have seasonal leaf fall i.e. in deciduous mesophytes the leaves are thin, whereas in evergreen mesophytes like conifers e.g. *Pinus*, the leaves are thick or leathery i.e. partly xeric ; this is because the leaves are exposed to alternate favourable and

unfavourable conditions throughout the year, especially in winter the soil is more or less physiologically dry (due to coldness) which does not allow easy absorption of solutes by roots.

5.10 Tropophytes : Schimper (1903, '35) introduced the term tropophytes for some terrestrial plants, which in opposition to hydrophytes and xerophytes, have deciduous leaves and "whose conditions of life are, according to the season of the year, alternately those of hygrophytes¹ and of xerophytes". The tropophytic vegetation is sometimes called *trophophilous*. The cold temperate flora is mainly trophophilous.

During summer or dry season, tropophytic flora behaves as a xerophyte ; the structure of their perennial parts becomes xerophilous. On the other hand, the flora behaves as hydrophyte during wet season or as mesophyte during winter. The leaves of tropophytes fall off according to seasonal variations. In winter they shed their leaves, this is due to winter cold. The shedding of leaves may also take place in summer, this is due to drought conditions. In case of conifers, where no shedding of leaves occurs, the persisting xerophilous leaves are sufficiently protected against cold and drought. The underground perennial parts of many rhizomatous herbs reappear again with the advent of monsoon even after the death of flowering shoot of such plants during winter. Thus the formation of underground stems is an important adaptation for the perennating buds to survive during unfavourable conditions.

In case of evergreen trophophilous woody plants e.g. *Ilex aquifolium* (Aquifoliaceae), the leaves are typically xerophilous i.e. protected by heavily cuticularised epidermis ; on the return of hydrophytic condition during the outbreak of monsoon, plants become adorned with dense masses of green foliage. So this type of periodical foliation and defoliation are characteristic of trophophilous flora. Besides, other structural modifications of tropophytes are (1) protection of winter buds, (2) covering of stems by thick cuticle, cork and leaf scars formed due to shedding of leaves and (3) efficient closing up of lenticels by the development of cork cells.

The monsoon forests, alpine and sub-alpine temperate flora, the teak forest of Burma etc. are tropophytic in nature. *Bombax malabaricum*—the silk cotton tree (Bombacaceae), *Spondias mangifera* (Anacardiaceae), *Shorea robusta* (Dipterocarpaceae), *Tectona grandis* (Meliaceae) etc. are examples of tropophytic plants.

5.11 Epiphytes : Epiphytes are the plants that seek accommodation in other plants but do not absorb food from them. The bond between the epiphytes and the plants on which they grow is less related. Most epiphytes grow upon various kinds of plants, some grow on the rock or even on the ground. Epiphytic flora of India ranges from thallophytes to highest phanerogams. In temperate regions of

Equivalent to hydrophytes—a term introduced by Schimper.

Himalayas all classes of epiphytes ranging from algae, lichens, mosses to pteridophytes and orchids are found.

In the plains of India, the epiphytic flora includes some algae, ordinary tree lichens and phanerogamic ones belonging to families Orchidaceae, Araceae, one or two species of *Ficus* (e.g. *F. ramenlacea*, Moraceae), Cactaceae and Polypodiaceae (ferns). The common epiphytic orchids are *Dendrobium*, *Vanda*, *Bulbophyllum*, *Rhynchostylis*, *Scindapsus*, *Raphidophora* and *Pothos* are general among Araceae. The only epiphyte belonging to Cactaceae is *Cereus flagelliformis*. Among the epiphytic ferns the important ones are *Vittaria* and *Drymoglossum*.

Adaptations :

Due to peculiarities in the habitat, different biological adaptations among epiphytes have been noted, these are :

The seeds of epiphytes as well as spores of pteridophytic epiphytes are of such structural peculiarities that they serve double object regarding their dispersal and fixation to the substratum. The seeds are light and very small (seeds of orchid, e.g. *Vanda*), or provided with long hairs and allied structures so that they may be easily conveyed by the wind on the trunks and branches where they are easily lodged in the fissures or holes. The fruits of epiphytic aroids e.g. of both *Scindapsus* and *Raphidophora* are fleshy berries which are eaten by birds and conveyed by them in their beaks for the lodgement on tree trunks.

Fixation of epiphytes to the trunks of trees is done by attaching climbing roots in case of *Scindapsus* and *Pothos*, in case of *Vanda* and other orchids by attaching roots known as clinging roots. *There is often division of labour between attaching and absorbing roots.*

Provision of water is a problem to the epiphytic phanerogams. because rain water soon flows off. Lower epiphytes e.g. lichens and mosses can absorb water present in mist and dews with the help of their whole surface. In Orchidaceae e.g. in *Vanda*, *Bulbophyllum*, *Dendrobium* etc. special aerial roots are developed, these roots are provided with spongy sheath—the so-called *velamen* by means of which they can absorb moisture from the atmosphere. In some of the orchids as in *Dendrobium* and *Vanda*, chloroplasts occur in the cortical tissue of the aerial roots. The structural modification of the epiphytic orchids varies according to the special type of situation to which they are adapted ; besides the aerial roots, they have roots which act as holdfasts. As water is not so much available, most epiphytic orchids of Bengal have xerophytic characters. In *Thecostele alata* (= *Cymbidium alatum*) there is reduction of leaf which is solitary on pseudobulb ; foliage leaves are very thick as in *Vanda* and *Rhynchostylis retusa*. This thickness of leaves is a provision against desiccation. So phanerogamic epiphytes are practically xerophytes.

In large climbing epiphytes like *Ficus ramentacea*, the leaves are also coriaceous and thick, the thick leaves are provisions against loss of water by transpiration. The leaf has multicellular epidermis which acts as water storage tissue.

In *Cereus flagelliformis* there is no foliage leaf, it has fixing as well as green aerial roots coming out from stem. In place of leaves there are numerous spines. The work of assimilation is done by succulent stems. In many cases hairs function as water reservoirs. In *Drymoglossum*, an epiphytic fern found in Sunderbans, hairs of most remarkable structures occur on roots. These hairs shrivel up during dry season, the protoplast in their cells withdraws to the base and shuts itself off from the dry part by cell wall. When rain falls, these hairs grow and become filled with water within a short time.

Food material is obtained by epiphytes in various ways ; carbon is taken from the air ; mineral matters and humus are accumulated within roots or within specialised leaves e.g. *pocket leaves*, *mantle leaves* as seen in some ferns like *Asplenium nidus*, *Polypodium quercifolium* etc.

The construction of the shoot and the whole structure of the epiphyte varies greatly. Some species like *Tillandsia usneoides* (Bromeliaceae) are rootless, some orchids such as *Polyrrhiza funalis* consist almost entirely of green roots. In *Dischidia* (Asclepiadaceae), one of the leaves forms pitcher ; this pitcher is provided with freely branching absorptive roots by the help of which the plant absorbs water from the pitcher.

The succulent habit of *Cereus flagelliformis* (Cactaceae) shows xerophytic character. The pseudobulbs in orchids are meant for storing water. Epiphytes have many structural features in common with terrestrial xerophytes, for these they must be adapted to endure prolonged drought.

According to mode of life, Schimper has divided epiphytes into four groups :

(a) *Proto-epiphytes*—those that find their nutrients in the cortex of their support e.g., species of Asclepiadaceae and few ferns.

(b) *Hemi-epiphytes*—those that send their aerial roots into soil e.g., some members of Araceae (*Scindapsus*, *Pothos*) and few epiphytic fig trees (*Ficus*).

(c) *Nest epiphytes*—those that collect moist humus within large interwoven mass of roots e.g., some orchids.

(d) *Tank epiphytes*—those whose leaves do the function of roots and absorb water and nutrient salts e.g., epiphytic members of the family Bromeliaceae (*Tillandsia*, *Nidularium*) etc.

5.12 Parasites : Parasites are the organisms which live on other plants and animals, deriving nutrients from them. The organism

on which they live and derive food is called *host*. Parasites among plants may be found in many bacteria, fungi and angiosperms. The host owing to the attack of parasite may be seriously injured and even ultimately killed.

In phanerogamic parasites, the modification of the organs is relative to the mode of parasitism. The commonest characters found in case of total phanerogamic parasite *e.g.*, *Cuscuta reflexa* (family Convolvulaceae) and *Cassytha filiformis* (family Lauraceae) are the complete disappearance of chlorophyll, reduction of leaves to scaly structures or the total disappearance of the leaves, slender stems with feebly developed xylem. Besides these, a special root-like sucking haustoria is developed at the point of contact of the parasite and the host. By means of haustoria *Cuscuta* and *Cassytha* suck food from the host. The host may be any shrubby or arboreal dicotyledon *e.g.* *Duranta*, *Lawsonia* etc. The penetration of haustoria may reach up to phloem. During germination, the seedling of *Cuscuta* makes no use of cotyledons as means of nourishment, the cotyledons remain undeveloped; after emerging from seed, the filamentous embryo makes a circling movement; if any suitable flowering plant as a host is found near about, it climbs that and at the point of contact produces haustoria. The seeds of *Orobanch* (Orobanchaceae), another parasite, germinate when they come in contact with the roots of the host plant—otherwise the seeds fail to germinate.

Many exotic phanerogamic parasites of the family Rafflesiaceae are so completely changed by their parasitic mode of life that they develop no apparent vegetative body at all but grow altogether within their host plants. But they often send out at intervals their extraordinary flowers. The vegetative body of such parasite is reduced to fungus-like mycelium. *Rafflesia arnoldi* is an example, its flower is the largest in the world, which comes out from the host. The mycelium-like tissue of *Rafflesia* ramifies through the cambium of the roots of the host. The flower buds are produced within the host and they ultimately break through the host during the time of flowering. Other phanerogamic parasites develop leaves and chlorophyll, they are called partial parasites; examples of such partial parasites are *Viscum album*, *Loranthus*, etc. of the family Loranthaceae.

5.13 Comparison between hydrophytes, xerophytes and halophytes regarding their adaptations

HYDROPHYTES	XEROPHYTES	HALOPHYTES
<i>Morphological :</i>		
1. No elaborate root system occurs. In total submerged aquatics, no root develops at all.	1. Large elaborate root system exists. Roots are mostly large tap roots penetrating great depths of soil.	1. Tap root system is not much elaborate and deeply penetrating. In many plants, roots are negatively geotropic. Formation of adventitious roots like prop and stilt is another important feature.

HYDROPHYTES

2. Most of the rooted and immersed hydrophytes have well developed, extensive, creeping underground stems (rhizomes) with profuse adventitious roots embedded in mud.

3. The stem is soft and tender. In most cases shoots have short condensed internodes.

4. The leaves show great variation in structure—the submerged leaves are thin, much dissected while aerial leaves are large, entire or slightly lobed.

XEROPHYTES

2. Stem is aerial, mostly erect but of limited growth; sometimes stem is metamorphosed into leaf-like cladode.

3. The stem is rigid and stout,

4. Leaves may be thin or rigid, fleshy and leathery. Extreme reduction of leaf surfaces into spines and allied structures or total absence of leaves are sometimes noted.

HALOPHYTES

2. Aerial stem of plants is well developed and much branched. In case of herbaceous plants, they are often prostrate.

3. The texture of stem ranges from soft to hard-woody type.

4. Leaves are thick and their surfaces are reduced, they are spatulate, oblong or scaly sometimes.

Anatomical :

5. Plant surfaces are not coated with any waxy or hairy coverings.

6. No development of cuticle on the epidermis of plant organs.

7. Stomata are either absent or when present they are restricted on the upper surface of leaves. Stomata are not sunken.

8. Stems and other plant parts are traversed by air cavities.

9. The mesophyll tissue is rarely or not at all differentiated into palisade and spongy tissues.

10. The xylem and woody lignified tissues in different plant organs are poorly developed.

5. Plants are coated with waxy and hairy outgrowths.

6. Plant organs are well cuticled.

7. Stomata are very often sunken—they are present on the lower surface of the leaves only. Size of guard cells is reduced.

8. Air cavities are absent; instead, presence of hypodermal water storage tissues is a marked feature in many cases. Mucilage is present in epidermal cells.

9. The mesophyll tissue is provided with very small intercellular spaces and often is not differentiated into palisade and spongy tissues but only palisade-like cells occur beneath both the epidermal layers.

10. Xylem and woody lignified tissues are largely developed.

5. Like xerophytes.

6. Like xerophytes.

7. Stomata are either sunken or lie at, or near the level of the lower epidermis.

8. Like xerophytes.

9. Like xerophytes.

10. Lignification of woody tissues is extremely poor.

HYDROPHYTES

11. Mechanical tissues are extremely reduced or not at all developed.

12. Glandular hairs and various types of secreting organs do not occur.

Physiological :

13. Rate of transpiration is less, excretion of water mainly takes place by guttation through hydathodes.

14. Due to weak light intensity, the growth of the submerged plants is reduced.

15. Gaseous exchange of submerged organs with the atmospheric air takes place by air communicating systems through stomata ; O_2 and CO_2 present in air cavities are used in respiration and photosynthesis respectively by internal circulation.

16. In most cases, absorption of water and mineral salts takes place by the entire permeable plant surface under water. Diffusion rate of dissolved gases (O_2 and CO_2) is slow due to reduced size and thickness of leaves

17. Vegetative modes of propagation by stolons and offsets are highly developed, seeds are less developed.

XEROPHYTES

11. Development of mechanical tissues with extensive lignification occurs.

12. Various types of glandular hairs and secretory organs are present.

13. Rate of transpiration is decreased or entirely checked by heavy cutinisation of epidermis and by the formation of sunken stomata.

14. Due to maximum utilization of carbohydrates in the formation of cell wall, the growth of plants is slow.

15. Gaseous exchange of both aerial and underground plant parts with the atmosphere takes place normally.

16. Absorption of water and mineral salts takes place by the help of long deep-seated root system—this is greatly enhanced by the development of high osmotic pressure and consequently a considerable amount of suction pressure.

17. Propagation takes place mainly by seeds.

HALOPHYTES

11. Mechanical tissues are less developed.

12. Hydathodes-like secretory organs are found to be present in many plants.

13. Like xerophytes, the rate of transpiration is checked by various kinds of morphological and anatomical modifications of leaves.

14. Growth of plants is normal.

15. Gaseous exchange of the aerial plant parts takes place normally but the respiration of underground parts i.e. roots takes place by the formation of negatively geotropic roots known as pneumatophores.

16. As the soil is physiologically dry like xerophytes, the absorption of water and mineral salts takes place slowly and selectively by the elaborate root system.

17. Propagation takes place by seeds. but seeds in most cases germinate viviparously.

CHAPTER 6

Ecological System (Ecosystem)

6.1 Definition and concepts of Ecosystem : Now-a-days ecology is mainly the study of ecological system or ecosystem. Ecosystem is essentially a technical term for 'nature' that was used previously by many ecologists. All the population of a given area i.e. the community or grouping cannot be separated functionally from the environment, rather both the community and the environment *function together* as a system what is known as *ecological system* or *ecosystem* (Whittaker, 1960 ; Odum, 1966). Hence to the view of modern ecologists, an ecosystem "is a functional unit where the biotic and abiotic components of the environment interplay" (Misra *et al* 1970). The community with all its plants and also animals forms the living i.e. *biotic part* of the ecosystem while the environment forms the nonliving i.e. *abiotic part*. Taxonomic components (biotic) in the ecosystem are termed as *ecological niche*. As the term habitat in ecology means the place where an organism lives, so the term ecological niche means the role that the organism plays in the ecosystem ; as for example, grasses, nongrassy herbs (forbs) and woody plants although not closely related taxonomically, occupy the same niche when present in grassland ecosystem (refer page 426).

The portion of the earth in which ecosystems operate i.e. the biologically inhabited soil, air and water, is called the *biosphere*. The earth upon which we live may be considered as a vast ecosystem. The biosphere obtains its energy from the sun and nonliving (abiotic) materials from the soil (lithosphere), water (hydrosphere) and air (atmosphere). For the study of ecology, this vast ecosystem may be classified into smaller units, the criteria for such classification should be climate, habitat, life-form of primary autotrophic components.

From the standpoint of ecosystem, a lake, a forest or any other recognisable unit has two biotic components, e.g. (a) an *autotrophic component* (autophyte)—able to absorb light energy from sun and manufacture food from simple inorganic substances and (b) a *heterotrophic component* (heterophyte) which utilises and decomposes the complex substances synthesised by the autotrophs. These functional components are arranged in overlapping layers on biosphere, the greatest autotrophic metabolism occur in the upper layer where light energy is available and the most intense heterotrophic activity takes place in the lower layer where organic matters accumulate much.

From the structural standpoint, four constituents comprising the ecosystem may be recognised for convenience, e.g. (1) *abiotic substances*

—these are basic and nonliving elements of the environment, (2) *producers*—the autotrophic organisms i.e. mainly green plants, (3) the large *consumers* or *macroconsumers*—heterotrophic organisms, mainly animals and (4) the *decomposers* or *microconsumers* (saprophytes)—heterotrophic organisms, mainly the bacteria and fungi that break down the complex substances of dead protoplasm (of producers), absorb some of the decomposed products and release simple substances for the use of new producers.

In the biosphere, the most common and extreme types of ecosystems found are : (a) terrestrial and (b) open-water aquatic systems. A terrestrial ecosystem (shown by field i.e. grassland) and an open-water aquatic system (shown by lake, pond or sea i.e. either fresh water or marine) are populated by different kinds of organisms.

In both the systems, the necessary units for function are : (1) abiotic substances e.g. basic inorganic and organic compounds ; (2) producers are vegetation on land while phytoplankton in water ; (3) macroconsumers i.e. animals are (a) grasshoppers, meadowmice etc. on land and zooplankton in water as direct or grazing herbivores, (b) soil invertebrates on land and bottom invertebrates in water as indirect or saprovores and (c) hawks and large fish as 'top' carnivores ; (4) decomposers are bacteria and fungi of decay. The large rooted plants are usually the autotrophs on land while microscopic floating plants (phytoplankton) are the autotrophs in deep water systems. Both types of autotrophs i.e. producers support similar forces of consumers and decomposers.

To understand the interplay of structure and function of biotic and abiotic part, the entire structure of an ecosystem is to be considered from different angles. According to Evans (1956), Whittaker (1960), Odum (1966) and others, the producer-consumer arrangement is one kind of structure called *trophic structure* (trophic=food). Again each "food" level is called *trophic level*. The amount of living organism (or material) in different trophic levels or in a component population is called the *standing crop*—this term equally applies to plants or animals. The standing crop of a population can be expressed in terms of *biomass* i.e., organism mass or in terms of the number per unit area. The standing crop generally represents population energy but it also provides *habitat* or living space for organisms, e.g. trees in a forest not only provide energy through food or fuel but they also modify climate and provide shelters for animals. The amount of abiotic materials like calcium, nitrogen, phosphorus etc. which are present at any given time may be termed as the *standing state* or *standing quantity*. The amount and distribution of both inorganic and organic materials present either in the biomass or in the environment are important factors in ecosystem. *Species structure* is another aspect of an ecosystem. *Species structure* means the number and kinds of species present in a community, the diversity of species (i.e. the relationship between the species and numbers of individuals or biomass) and the spatial arrangement of individuals of

each species in the community. Ecosystem can be studied in various units i.e., a small pond, a large lake, a tract of forest etc. can provide a suitable unit of study.

6.2 Some important Ecosystems of the World

I. MARINE i.e. SALT WATER ECOSYSTEM (THE SEAS, ESTUARIES AND SEA-SHORES)

A. *The Seas*—The major oceans like Indian, Pacific, Atlantic etc. cover almost 70% of the earth's surface. Seas are the largest and most congested of ecosystems, as phytoplankton under every square meter and other living organisms extend to the greatest depths. Various types of adaptations are exhibited by marine organisms e.g. ranging from tiny plants having floating devices on the upper layers of water to the giant deep-sea fish having huge mouth and stomachs that live in dark and cold water layers. The autotrophic layer i.e. photic zone (lighted zone) is much smaller in comparison with the heterotrophic i.e. euphotic zone so that the nutrient supply in the former is limiting. Some physical factors like waves, tides, currents, salinities, temperatures, light intensities etc. dominate life in ocean; they largely determine the makeup of biological communities. These biological communities, in turn, have some influence on the composition of bottom sediments and gases in solution. In sea, the *food chains*¹ begin with the tiny autotrophs (phytoplankton) and end with the largest heterotrophs (animals like giant fish, squid, whales etc.).

B. *Estuaries and Sea-shores*—Between the sea and different land marks near about, various types of ecosystems having ecological characteristics of their own are noted. Estuaries are the river mouths or coastal bays where the salinity is medium i.e. intermediate between the sea and fresh water and where the tidal action is an important physical regulator. Estuaries and sea-shores are most fertile and hence packed with life—this is due to much better food conditions and much more variable physical factors (salinity, temperature etc.) in those regions than the sea itself. Odum (1965) has recognised five mechanisms and conditions that maintain biological energy flow in those regions, these are—(1) tidal action, that maintains a rapid removal of waste products of metabolism; (2) a variety of plant species and life-forms that provide a continuous photosynthetic process. To maintain such a higher process, three major life-forms of autotrophs are recognised viz. (a) *phytoplankton*, (b) *benthic microflora*—algae inhabiting in and on mud, sand, rocks and bodies of animal shells, and (c) *large attached plants* like seaweeds, submerged grasses and emergent marsh grasses; (3) an estuary often functions as an nutrient trap; (4) primary production by a succession of crops throughout the year and (5) close contact between autotrophic and heterotrophic layers.

¹ "The transfer of food energy from the source in plants through a series of organisms with repeated stages of eating and being eaten is known as the *food-chain*."

II. FRESH WATER ECOSYSTEM :—This type of ecosystem is represented by streams, rivers, springs, lakes, ponds, pools, swamps etc. The fresh water bodies are characterised by typical biotic communities and abiotic environments mainly because of plenty of water both in external and internal environment of organisms. In fresh water ecosystem, the water bodies may be running i.e. *lotic* as seen in streams, rivers, springs etc. and standing i.e. *lentic* as seen in pools, ponds, swamps etc. On the basis of the depth of water and available light, large ponds and lakes are divided into distinct zones viz, (a) *littoral zone* which contains rooted vegetation along the shore, in this zone light reaches up to the bottom ; (b) *limnetic zone* of open water dominated by plankton, in this zone available light is at compensation point and (c) *profundal zone*, it is a deep water zone containing only heterotrophs—here the light is below the compensation point. Often lakes become thermally stratified during summer and again in winter due to temperature differences ; the upper warm layer is known as *epilimnion*, this layer is rich in plants and here water always keeps on circulating. The lower cool noncirculating layer is the *hypolimnion*, generally devoid of plants. Between the epilimnion and the hypolimnion, there lies a transitional layer called *thermocline*—this layer acts as a barrier to exchange of materials. On the basis of fertility and productivity lakes are often classified into two types e.g. (1) *oligotrophic*—deep lakes, poor in nutrient level and productivity and (2) *eutrophic*—shallow lakes, rich in nutrients and productivity. The biotic organisms in lakes may be classified, on the basis of size and habit, into five types, viz. (a) *macrophytes*—large plants, (b) *planktons*—small, free-floating organisms that float according to the direction of water current, (c) *nektons*—organisms that are able to swim at their will, (d) *neustons*—organisms (both resting and swimming types) that are confined to the water surface and (e) various types of other *macrofauna*.

III. DESERT ECOSYSTEM :—This type of ecosystem is noted in regions where annual rainfall is less than 254.0 mm or in hot regions where there is more but unevenly distributed rainfall throughout the year. Bushes and cacti are conspicuous in deserts. Generally four distinct types of life-forms of plants are found in desert ecosystems such as (a) annuals, represented by *Bromus* species that avoid drought by growing in presence of adequate moisture, (b) the desert shrubs, with numerous branches arising from basal part of the short stem and small thick leaves that may be shed during dry periods—these desert shrubs survive by their ability to become dormant before wilting takes place, (c) the succulents e.g. cacti and euphorbias—these plants store water in their water storage tissues, and (d) microflora e.g. mosses, lichens, some blue-green algae etc. which remain dormant in the soil during dry period but they are able to respond quickly to cool or wet periods. Among animals, reptiles and some insects are well adapted to deserts. Of the mammals, a few species of nocturnal rodents and camels are well adapted ; the former can live in deserts without

drinking water while the latter, though drink water, are able to store water in their bodies.

IV. GRASSLAND ECOSYSTEM :—Grasslands are one of the most important of terrestrial ecosystems, which generally occupy 19% of the total world vegetation. Natural grasslands occur in regions where the precipitation is intermediate between that of desert lands and forest lands. In temperate grasslands the annual precipitation lies between 254.0 mm and 760.0 mm. The climate of temperate grassland is determined largely by temperature, seasonal distribution of rainfall and water holding capacity of the soil. Tropical grasslands may have 1,520.00 mm annual rainfall in a wet season which alternates with a prolonged dry season.

In grassland ecosystem, the primary producers i.e. dominant life-forms of plants are grasses which range from tall (1.5 m—2.5 m) to short (0.5 m or less) species that may grow in clumps or with underground rhizomes. Large variety of forbs (nongrassy herbs) and woody plants (trees and shrubs) also occur in grasslands either as scattered individuals forming so-called "savannah" or in belts or groups along rivers and streams.

Large herbivores (mostly mammals), a characteristic feature of grasslands, are the dominant consumers. Besides mammals, large grazing birds and insects are also found as consumers. The soil is rich in humus and microbes ; in tropical grasslands the activities of decomposers increase during the rainy season.

Now-a-days, it is very difficult to locate the natural grasslands. The natural grasslands all over the world have been affected largely by man's multifarious activities and as a result much of the area has been converted to agricultural land.

Based on the floristic composition, Whyte (1957) has classified the grasslands of India into eight types as follows :—(1) *Schima-Dichanthium* type on black soils, (2) *Dichanthium-Cenchrus* type on sandy loams, (3) *Phragmites-Saccharum* type on marshy localities, (4) *Bothriochloa* type on paddy tracts and high rainfall belt, (5) *Cymbopogon* type on low hills, (6) *Arundinella* type on high mountains, (7) *Deyeuxia-Arundinella* type in mixed temperate climate and (8) *Deschampsia-Deyeuxia* type in mixed temperate alpine climate. The first four types are the characteristic of the plains and the last four types of the hills and mountains.

V. CROPLAND ECOSYSTEM :—This is a man-made ecosystem. Hence cropland ecosystem is an artificial one which originates from natural terrestrial ecosystems of forests, grasslands and even deserts due to man's multifarious activities. In this ecosystem, man tries to control the biotic as well as abiotic environment, specially edaphic factors, for growing specific plants like paddy, wheat, corn etc. Forests and grasslands are converted into cropland or single species plantations. Under proper management, crops are normally single species stands.

VI. FOREST ECOSYSTEM :—Like open sea, forest forms the extreme type of ecosystem in biosphere regarding standing crop biomass and the relative importance of physical and biological regulation. In this type of ecosystem, well-ordered and lengthy ecological succession with herbaceous plants is the characteristic feature. A variety of vegetations representing stages in succession and adaptations to varying soil and moisture conditions of the substrate may be noted in any forest region.

The northernmost forests, as seen in temperate zones of eastern and western Himalayas, are characterised by evergreen conifers composed of genera *Picea*, *Pinus*, *Abies* etc. Here the species diversity is low, often with a few species of trees forming pure stands. Moist deciduous forests are characteristic of the Deccan plateau and some areas of sub-Himalayan tracts extending from the Punjab in West to the Assam valley in the East. Northern Punjab is characterised by temperate (dry) deciduous forests. These forests have more pronounced stratification and a greater species diversity. The third type, the tropical forests range from broad-leaved evergreen rain forests to tropical deciduous forests. Two types of life-forms e.g. *lianes* and *epiphytes* are characteristic of tropical forests. Here the species diversity reaches a maximum, there may be more species of plants and insects in a few areas of tropical rain forests.

CHAPTER 7

Zonal Distribution of Plants

The different types of plant communities met with in various parts of the earth, form distinct zones of vegetation according to geographical belts of the world. Such zones of vegetation are as follows :—

A. TROPICAL ZONE

1. Tropical woodland

- (a) *Rain forest or evergreen forest*
- (b) *Monsoon forest or moist deciduous forest*
- (c) *Thorn forest and thorn-bushland*
- (d) *Littoral forest*

2. Tropical and sub-tropical savannahs

3. Tropical desert

B. TEMPERATE ZONE

- (a) *Deciduous forest*
- (b) *West temperate forest or sholas*

C. ARCTIC OR FRIGID ZONE

7.1 Tropical Rain Forest or Evergreen Forest : In equatorial countries e.g., Belgium Congo, Amazon valley, Java, Malaya i.e., countries near about the equator, there is a belt of forest which has retained its original character and is known as tropical rain forest.

In tropical rain forest the atmosphere is excessively humid, annual rainfall exceeds 5000.0 mm per year. The soil consists of rich humus. During day, great heat prevails.

Tropical rain forest exhibits luxuriant vegetation with abundant species which struggle for utilization of space.

In tropical rain forest one finds as if plants piled upon plants showing storeys. The highest trees with thick trunks are unbranched up to the height of 33.5m or more, beneath them trees of moderate stature occur ; next slender or thick-stemmed palms of every type, tall ferns etc. occur. All sorts of lianes (climbing plants) and epiphytes grow in abundance. Herbs are comparatively rare in comparison with the trees and woody shrubby lianes. The trees belonging to the families Leguminosae, Moraceae, Myrtaceae, Lauraceae, Palmae are predominant. Of the Moraceae, there is great number of species of

Ficus. The shrubs belong mainly to the following families which are predominant such as Urticaceae, Rubiaceae, Araceae (*Scindapsus*, *Pothos*) etc. Epiphytes belong to Orchidaceae mainly and Araceae. Of the palms species of *Calamus* are predominant. Root- or plank buttresses are often found in large trees belonging to the families Sterculiaceae, Myrsinaceae etc. also occur.

Among the cryptogamic flora, ferns of many types grow ; the chief family is the Hymenophyllaceae. Besides this, the leaves and trunks of trees are beset with lichens, mosses etc. The characteristic feature of the tropical rain forest is the luxuriant abundance of epiphytes of various types.

Due to admixture of various species, the tropical rain forest forms a comprehensive community. In tropical rain forest, associations formed by single dominant species are very rare.

Adaptations of flora : In many plants like *Sterculia alata*, species of *Ficus* etc. plank buttresses are formed by roots ; these buttresses provide additional support to the trees.

Thorny stems are found in many genera e. g., *Erythrina*, *Hura* etc. The periodic habit of development characterised by resting period, which is distinct in other plant communities, is wanting in plants of tropical rain forest as there is neither summer nor winter ; formation of new leaves and blossoming goes on throughout the year.

The leaves are provided with drip tips e.g, *Ficus religiosa*—this is an adaptation for draining off excess of water from the leaf surface. The leaves of trees, in most cases, have upward and downward position so that rain water cannot accumulate on the leaf lamina.

As the rainfall is violent, device for protection against injury by mechanical action of rain exists in plant organs such as by the formation of strong and coriaceous leaves with stout blades. In the members of Leguminosae, leaves are compound, so the surface are less exposed to the action of wind and rain. In some plants leaves are tough and are provided with folds and wrinkles. The huge leaves of palms and aroids have large sheaths which also function as protection against mechanical action of wind and rain.

TROPICAL RAIN FORESTS IN INDIA—Indian tropical rain or evergreen forest is divided into two sections viz, one which comes under the influence of the main south-west monsoon and the other i.e. of the Karnatic, which depends on the much weaker winter or north-east rains. The former type occupies the West coast extending from North Kanara to the South and in the eastern sub-Himalayan tract in Assam. The vegetation contains trees of many families among which Dipterocarpaceae, Guttiferae, Lauraceae, Magnoliaceae, Anonaceae, Meliaceae, Burseraceae, Sapotaceae, Euphorbiaceae, Anacardiaceae and Palmae are dominant. Climbers and other woody lianes are plentiful, epiphytes and climbing palms are also abundant—they all show prolific growth. Calder writes that “the evergreen

forests provide in the main no exception to the rule of absence in India of a species dominant over a wide area; but some of its members, e.g., *Dipterocarps* show nevertheless a tendency to the gregarious habit." *Dipterocarpaceae* contains many species of economic importance e.g. *Dipterocarpus indicus*, *Hopea parviflora* etc. Other plants occurring are *Mesua* spp., *Calophyllum tomentosum*, species of *Cedrela*, *Dalbergia*, *Bischofia* and *Artocarpus*. Bamboos are plentiful and associated with them are to be found Teak, Rosewood and Ironwood. According to Rowntree (1954), Assam rain or evergreen forest shows six principal associations, these are (a) *Dipterocarpus Mesua-Michelia* association, (b) *Cinnamomum-Amoora* association, (c) *Bischofia-Dillenia* association, (d) *Shorea-Lagerstroemia* association, (e) *Tetrameles-Stereospermum-Cedrela* association and (f) *Dillenia-Lagerstroemia* association. Various types of tree ferns also occur among pteridophytes. The Karnatic evergreen forests on the other hand are characterised by their comparatively small size and harder texture. Here species of *Mimusops*, *Melia*, *Tamarindus* etc. are found. The families Ebenaceae, Sapotaceae, Rhamnaceae, Capparidaceae and Myrtaceae become prominent.

Chaudhuri (1967) has reviewed the tropical evergreen forests of India, Burma and Ceylon. In south Tenasserim of Burma, where the rainfall is 3000.0 mm and the soil is deep, *Dipterocarpus* species form the main crop of the top canopy. The second top *Dysoxylum grande* forms a mixture with *Swintonia floribunda*, *Michelia champaca*, *Melanorrhoea glabra* and *Baccaurea sapida*. In Peguayoma forests species of *Amoora* forms the second top in *Dipterocarpus* forests. Evergreen forests of Ceylon are characterised by *Chukrasia velutina* which occurs along with members of Anacardiaceae and Anonaceae. Western Ghat tropical evergreen forest is seen in N. Kanara, Agumbi, Mukut, Karianshola of Anamalais, Palghat hill range etc. This forest is dominated in different places by *Chukrasia tabularis*, *Dysoxylum malabaricum*, *Aglai roxburghiana*. Northern tropical evergreen forest ranges from Assam, Chittagong hill tracts and North Bengal. The North Bengal evergreen forest is dominated by species of *Dysoxylum*, *Amoora*, *Chukrasia*, *Toona*, *Aglai*, *Terminalia myriocarpa*, *Michelia champaca*, *Phoe heinesiana* etc. In the Chittagong hill tracts and northern Aracan *Dipterocarpus* forests predominate. In the upper Assam, on the lower slopes of Mishmi, Abor, Daphla, Aka, Manipur and Lushai hills and Naga, *Dysoxylum binectariferum*, *Toona ciliata* and *Amoora wallichii* occur with *Dipterocarpus*, *Acrocarpus*, *Shorea*, *Mesua*, *Michelia* etc. In the lower hills and hill slopes of Cachar, Khasia and Jaintia hills *Amoora*, *Aphanamixis*, *Dysoxylum*, *Chukrasia* occur along with many other evergreen species.

7.2 Moist Deciduous Forest or Monsoon Forest : This type of forest occurs in the tropical countries with average rainfall of 1,500-2,000 mm per annum and prolonged dry season alternating with wet season. In India, deciduous forest covers an extensive area occupying a strip along the western side of the Deccan plateau i.e. Bombay, North-east Andhra, Madhya Pradesh, Gangetic plain and some

areas of the sub-Himalayan tract, extending from the Punjab in the West to the Assam valley in the East. Deciduous forests also occur in Burma and in some parts of Ceylon.

The vegetation is composed mainly of trees which remain leafless in dry season extending over the period from December to May. The trees are tall with an average height of 20-30m. The arboreal vegetation in the monsoon or deciduous forests practically consists of tropophytes, assuming mesophytic and xerophytic characters in the alternating wet and dry seasons respectively. In this forest Bamboos occur plentifully, they are located between the interspaces of tall trees. The lianes belonging to families Menispermaceae, Vitaceae and Papilionaceae also occur on tree tops and other herbaceous plants. From the forester's point of view, deciduous or monsoon forest is the most important type, as it is the main source of supply of Teak (*Tectona grandis*), Sal (*Shorea robusta*) of the sub-Himalayan tracts, the Padauks (*Pterocarpus indicus*) and the Sandalwood (*Santalum album*) of Mysore, Coimbatore and adjoining country and of Anjan (*Hardwickia*)—the hardest and heaviest of Indian woods. Besides these, important species of the genera *Terminalia*, *Lagerstroemia*, *Albizia*, *Anogeissus*, *Soyimida*, *Chloroxylon*, *Swietenia*, *Diospyros*, *Acacia*, *Dalbergia* and others occur.

In moist Siwalik sal forests, *Toona ciliata* and *Trichilia connaroides* occur here and there. In the Tista valley slopes of N. Bengal, *Toona ciliata* forms 2.1% of crop. In the dry mixed pockets, *Dysoxylum binectariferum* and *Aphanamixis* form 1.0% and 8.5% of crop respectively. In the moist deciduous forests of the Jalpaiguri division of W. Bengal, *Aphanamixis*, *Chisocheton* and *Amoora* species occur with *Schima wallichii*, *Litsaea* spp., *Machilus* spp., and *Trichilia connaroides* occurs here and there along with *Lagerstroemia*, *Callicarpa* spp. etc. In the dry mixed sal forests of Kurseong division of W. Bengal, *Toona ciliata*, *Amoora wallichii* and species of *Aphanamixis* predominate together with *Chukrasia tabularis* in the top storey.

The ecological adaption of the flora consists in the capability of the plants to cope with and face the dry season, usually in the month of December, sometimes up to may which is accompanied by dry winds to which the plants are exposed; consequently trees lose their hydrophilous foliage during the approach of the dry season and renew them at or immediately before the beginning of the monsoon rains. Due to the spreading of the tree branches in the horizontal direction, most of the trees assume the shape of an umbrella—this is a protection against dry wind action.

7.3 Dry or Temperate Deciduous Forest : This type of forest occurs mainly in the northern Punjab where the rainfall does not exceed 75.9 cm and not less than 50.5 cm. The growth-form of trees is open; the important species occurring are *Albizia lebbek*, *Dalbergia sissoo*, *Acacia arabica*, *A. modesta*, *Prosopis spicigera* etc. The adaptations are more or less like those of moist deciduous forest type.

In other parts of India, temperate deciduous forests are found in Madras, North Kanara and in Bhandera division of Madhya Pradesh.

Madras dry deciduous forests are dominated by *Soymida febrifuga*, other species that occur along with them are *Terminalia* spp., *Tectona grandis*, *Pterocarpus marsupium* etc. *Soymida febrifuga* forms the top storey both in North Kanara as well as in Bhandera division of Madhya Pradesh dry deciduous forests.

7.4 Thorn Forest : Warming has described this type of forest under thorny savannah-vegetation which is composed of (a) *orchard-scrub*, and (b) *thorn bushland* and *thorn forest*. Thorn bushland and thorn forest are generally formed where the shrubs stand closer together with orchard-scrub (a formation of little trees up to 4m in height which are richly armed with thorns and for the most part have ternate or pinnate leaves, but are leaflets during dry season).

Thorn forest and thorn-bushland are wide spread over the tropics where the rainfall is not considerable i.e. less than 75.9 cm. Thorny forest is composed of many species, of which 'acacias' form predominant species; despite prolonged drought, epiphytes also grow in large number. A few herbs also occur here and there.

Characteristics of plants are a thick cuticle or a coating of long persistent hairs, the small development of leaf surface and the change of leaves and stems into spines or thorns. On the other hand, species of *Acacia* and other Leguminosae guard against complete desiccation by the closing together of thin leaflets. Thorn bushland and thorn forest are very much widespread in the drier parts of Africa and Asia. In India, thorn forests are found in Chittor, central Salem and some parts of Madhya Pradesh. *Azadirachta* species form an important association in the top of the forests of Chittor and central Salem. Betul forest of Madhya Pradesh is rich in *Soymida*. In Madhya Pradesh thorn forests, species of *Acacia*, *Balanites*, *Capparis*, *Azadirachta* etc. are found.

7.5 Littoral or Tidal Forest : Refer article 5.6B, page 405

7.6 Tropical and Sub-tropical Savannah : Tropical and sub-tropical savannahs contribute together to the formation of *true savannah*. Savannah is a vast stretch of xerophilous grassland mixed with scanty arboreal and shrubby vegetation; it is closely allied to steppe¹. Savannah generally occurs in the rainy tropical and sub-tropical regions of the world.

The vegetation has only one resting period i.e. the dry season, during which the scattered trees remain leafless—so plants are endowed with xerophytic and semi-xerophytic characters. During dry season, the savannah is often devastated by fires; at the commencement of rainy season following summer, all the vegetation becomes fresh green and clothes itself with rich blossoms.

¹ Steppe is only a pure grassland without trees.

The majority of plants are tall grasses which have coarse and stiff leaves, they grow in tufts to a variable height ranging from $\frac{1}{3}$ rd of a metre or more. Sometimes members of Cyperaceae are also found together with Gramineae. In addition to grasses and in contrast with true steppe, shrubs and trees accompanied by a few lianes and epiphytes are also present.

True savannahs are found in southern part of N. America, Brazil, Venezuela, Congo, Cameroon, Ceylon, Burma and India. According to climatic regions, savannah may be tropical and sub-tropical.

INDIAN SAVANNAHS—In India neither true tropical savannah nor vegetation like that of true savannah is found. Here the savannah is degraded high forest communities subject to changes by continuous biotic activities. According to Champion, a kind of degraded riverain forest closely resembling savannah occurs in India and there are four main types of such vegetation viz., (a) *North Indian upper alluvial savannah*, (b) *North Indian lower alluvial savannah*, (c) *Dry savannah* and (d) *Nilgiri sub-tropical dry savannah*.

North Indian upper alluvial savannah is also known as 'Sal' savannah. It occurs all over the Gangetic plain including lower Brahmaputra valley. It is degraded sal forest in which *Shorea robusta* (Sal) predominates in groups together with *Lagerstroemia parviflora*, *Bombax malabaricum*, species of *Adina*, *Lannea* etc. Like true savannah, grasses occurring are tall and crowded; they are represented by *Narenga porphyrocoma* (1.5-2.5 m high), *Cymbopogon nardus* (up to 8 m), *Themeda gigantea* (2.3 m) etc.

North Indian lower alluvial savannah is also like that of upper alluvial savannah; its vegetation is also identical with that of former type except the occurrence of occasional dense patches of shrubby *Zizyphus* and *Erianthus* species.

Dry savannahs are found throughout the deciduous forests, here trees occur in small patches with dense grassy under-growth.

Nilgiri sub-tropical hill savannah generally exists on the slopes of Nilgiri and Palni hills between altitude of 1000 and 2000 m. The flora is chiefly composed of tall grasses and deciduous scattered trees, the tree i.e., arboreal vegetation is represented by *Dalbergia latifolia*, *Embelica officinalis*, *Phoenix humilis*, *Anogeissus latifolia* etc.

SAVANNAH OF BURMA—Kurz (1877) in his "*Forest flora of Burma*" has mentioned the jungles of Burma as *savannah-forest formation*. Savannah-forest formation originates in favoured spots when savannah-trees aggregate more closely and other trees become infiltrated to them. The ground is heavily clothed with grass and perennial herbs. Savannah forest of Burma is also known as *bush-forest*.

SAVANNAH OF CEYLON—According to Pearson (1899), the savannah of Ceylon is known as *patanas*. Patanas are xerophytic grassy slopes and plains of considerable area covered with various

species of grasses belonging to the genera *Panicum*, *Paspalum*, *Aristida*, *Sporobolus* etc. Tree or arboreal vegetation is entirely represented by few species of the families Myrtaceae and Euphorbiaceae. Ceylon patanas are of two categories viz., *moist* and *dry*. Dry patanas are closely related to American savannahs and occupy altitudes less than 1,500 m ; above this altitude moist patanas occur. Abnormal climatic condition and grass-fire play an important role in the conversion of savannah-forest into savannah.

7.7 Tropical Desert : It occurs in regions where rainfall is very scanty and irregular. The rainfall is continuously lacking for a long time during the season, hence the scantiest vegetation can only exist. In desert little greyish-green plants occur here and there and which stand wide apart, the intervening large stretches of soil are normally devoid of vegetation.

The atmosphere of the desert is very dry, the annual rainfall is below 22 cm ; there are extreme variations between the seasonal as well as day and night temperatures *e.g.*, in a typical desert during the month of June, the day temperature may reach about 40-46°C while night temperature records 0° to 2-3°C.

The soil in a desert is not uniform, it may be pure sandy forming vast stretches of sand and dunes, solid rocky or stony and gravelly (due to disintegration of solid rock by the action of the sun and the wind). Hence the vegetation of desert varies according to the nature of soil and the availability of moisture. Desert vegetation is mainly xerophytic but regarding the degree of xeromorphy, the habit and the structure of desert flora are greatly influenced by the peculiar conditions of climatic and edaphic factors.

The vegetation of desert is ephemeral type *i.e.* of short duration. There are two ecological types of flora occurring in the desert such as (a) flora depending directly on rain and (b) flora depending on underground water ; in the first type, plants are mostly ephemeral. The plants of the second type are perennial mostly having long root system for search of water under great depth.

In India, the desert regions are situated in Rajasthan, *e.g.* Thar desert.

ADAPTATIONS IN DESERT : (1) *Rapidity of development* of vegetation after the first showers of rain and the commencement of spring.

(2) *Morphological features* are of extreme xerophily such as reduction in size or arrest of leaves, formation of aqueous tissues in stem or leaf, sunken stomata, thick-walled epidermis and strong development of cuticle, hairy coating etc.

(3) *Rolling plants in desert.* In deserts, some species of plants break loose from the soil and are buffeted hither and thither—those plants are called rolling plants. In East Indian dunes, species of *Spinifex* are typical examples of such plants.

(4) *Hygrochasy*. This is the phenomenon in which different plant parts like stems, fruit-stalks, valves of fruits, bracts etc. are *closely curled* towards one another when dry but *open apart* when moistened. By this method seeds are scattered during moist season.

A. VEGETATION OF RAJASTHAN DESERT :

Rajasthan desert region includes Jaisalmir, Jodhpur and Bikanir in the West comprising about 65,000 sq. miles ; other States lying towards East such as Kotah, Ajmer, Dholpur etc. are semi-arid having an annual rainfall of 400-600 mm per annum, whereas Jaisalmir, which represents the aspects of true desert, has an average rainfall of 250 mm per annum.

Rajasthan desert vegetation consists of Indo-Malayan as well as perso-Arabian and African elements. Here the vegetation exhibits three distinct communities e.g., (a) sand community, (b) gravel community and (c) rock community.

(a) *Sand community*—This type of community is noted in greater portion of W. Rajasthan covered with sand and sand dunes which by wind action (blowing to South-West and North-East direction) are subject to shifting plants here and there. In this region psammophytic community is met with ; many species cannot be fixed there owing to the frequent drifting and shifting of sand by wind action. On dunes hardy species such as *Calotropis procera*, *Indigofera argentea*, *Leptodenia spartium*, *Aerva pseudotomentosa* etc. are found scattered here and there. *Panicum targidum* is dominant grass of this region. The plants are provided with exceedingly long branched roots with tufted habit—this adaptation is meant for shifting sand ; *Aerva pseudotomentosa* is found as dominant on expanded plain. On the top of dune the most important plant *Calligonum polygonoides* is found to grow. Among sand loving species of Gramineae, *Panicum* and *Pennisetum* occur. The common and most important stoloniferous Cyperaceae is represented by *Cyperus arenarius* which forms mat-like vegetation on sand.

(b) *Gravel community*—Gravel or coarse sand community occupies a large areas of Jaisalmir and near about areas. The soil forms firm surface layer and has poor water retaining capacity. Plants of this community have prostrate habit with stiff woody branches. Shrubby bushes are represented by *Sarcostemma pauciflora*, *Anticharis linearis*, *Blepharis scindicia*, species of *Barleria*, are common in this region. Among other plants, the most common are tufted stoloniferous grasses such as species of *Aristida*, *Pappophorum*, *Eleusine* etc. *Tribulus terresteres* and species of *Fagonia* (belonging to the family Zygophyllaceae) with deep penetrating roots and decumbent habits form the typical mat vegetation on gravel. Gravel association at Bap to Jaisalmir consists of *Boerhavia diffusa*, *Cleome papillosa*, *Fagonia eretea*, *Aristida mutabilis* etc. Some members of Asclepiadaceae such as *Calotropis procera* and *Leptadenia spartium* are also met with in this community.

(c) *Rock community*—Except small isolated hills, the greater portions of Jaisalmir and Jodhpur of Rajasthan are covered by rocks. There are three rocky hill areas, viz. (1) Kailana-Jodhpur-Mandar plateau consists of red sand stone, (2) Jaisalmir plateau consists of both sand stone and limestone and (3) the Burmar hills consist of igneous rocks i.e., rhyolite.

The common shrubs occurring in three areas are *Euphorbia nerifolia*, some species of twining shrubs like species of *Convolvulus*, *Sarcostemma* etc. Other xerophytic plants viz *Capparis dicidua*, (Aizoaceae), *Bouchea marrubifolia* represent the rock vegetation of those areas. Some lithophytic grasses e.g. species of *Aristida*, *Elionurus* etc. are also found to grow there. The trees are very few, they are dwarf and have gnarled outlook.

The most important factor noted in the rock community is the presence of ephemeral heterogeneous herbs which after a shower suddenly burst forth into blossoms and complete their life cycle including flowering and fruiting in less than a month.

Rajasthan desert vegetation is typically xerophytic, consisting of all the four types of xeric habits viz. drought escaping, drought enduring, drought evading and drought resisting. To the first category, belong all ephemeral herbs which blossom suddenly after a shower. Species of *Calotropis*, *Indigofera* and other bushy shrubs are drought evading—these plants evade drought with the help of long deep penetrating root system and stunted growth. Drought resisting plants are represented by succulent herbs e.g., *Euphorbia nerifolia*—they can resist drought by storing water in tissues. Plants adapted to sand dunes have tufted or prostrate habit with long branched stolons giving rise to branched long roots. Most of the plants, belonging to all categories, have palisad tissue developed on the lower side, to avoid intense illumination caused by reflection from the surface of sand.

7.8 Evergreen Coniferous Forests : Coniferous forests occur in most diverse climates, still these are extensively distributed in cold temperate zones. In India evergreen coniferous forests occur in temperate zones of eastern and western Himalayas including Sikkim where the altitude ranges from 2,000 to 4,000 metres. Sometimes some members of coniferae reach above 4,000 m but do not form dominant flora there. The characteristic vegetation is mainly composed of coniferous trees e.g., *Pinus excelsa*, *P. khasya*, *Cedrus deodara*, *Picea morinda*, *P. smithiana*, *Abies pindrow*, *A. webbiana*, *A. densa*, *Tsuga brunoniana*, *Taxus baccata*, *Larix griffithii*, *Cryptomeria japonica* and *Juniperus* spp. together with other species like *Quercus*, *Betula*, *Castanopsis* etc. of angiosperms.

Dwarf shrubs and undershrubs in association with conifers are also numerous. In eastern Himalayan tracts and Sikkim they are represented by species of *Rubus*, *Berberis*, *Cotoneaster*, *Ilex*, *Spiraea*, *Hydrangia*, *Hypericum*, *Polygonum* etc.; other associated trees are

species of *Bucklandia*, *Alnus*, *Betula*, *Castanopsis*, *Quercus* etc. In the coniferous forest zone of western Himalayas, *Picea smithiana* and *Taxus baccata* form pure communities of conifers; the main broad-leaved angiospermic trees and shrubs are *Juglans regia*, species of *Prunus*, *Aesculus*, *Acer*, etc. Plants having creeping rhizomes, stolons or roots producing buds are also found associated with coniferous forests—they are represented in eastern Himalayas by *Vaccinium numularia* (Vacciniaceae), *Hydrocotyle javanica* (Umbelliferae), species of *Gaultheria* (Ericaceae) etc.

The evergreen forest consisting mainly of coniferous vegetation forms the 'coniferous forest.' Hence coniferous trees are generally distinguished ecologically from summer green, broad-leaved trees by the xerophilous structure and consequently lesser rate of transpiration. The leaves of coniferous trees are not shed. Their morphological characters correspond with xerophytes in which too much loss of water by transpiration is checked. According to Stopes (1907), the xerophytism in the coniferae is due to the presence of tracheids in the wood and which have lesser water conducting capacity than that of tracheae or vessels—so the xeromorphy is not due to ecological conditions but due to poor conduction of water.

The endurance of shade by coniferous trees like *Picea*, *Abies*, *Taxus*, *Thuja* etc. is the most important factor—they can grow and survive in weak light and shade. This phenomenon is known as 'tolerance'.

In warmer regions, coniferous forest becomes less prominent. The soil on which coniferous vegetation grows is physiologically dry. In cold regions, coniferous forest grows on all types of soil ranging from dry rocks, sandy rocky soil to wet rocks.

7.9 Wet Temperate Forests or Sholas : Sholas are evergreen temperate forests of close canopy. This type of forest occurs in South India viz. in Ootacamund and its vicinities of Nilgiris, Malabar region, Annamalai, Palni and Tinnevely hills above the altitude of 2,000 m. The vegetation consists of all types of arboreal, shrubby and herbaceous plants. Arboreal vegetation is mainly composed of medium sized (15-20 m in height) trees. The tree trunks are covered by epiphytic ferns, mosses and lianes of various types; the leaves of such trees are in dense crowns and leathery with red colours.

Up to an altitude of 800 m, shrubs and herbs belonging to families Rubiaceae and Compositae together with some members of Acanthaceae e.g. *Stenosiphonium rasselianum* are plentiful. Above 800 m, the vegetation is chiefly herbaceous and is composed of *Kalanchoe*, *Vernonia*, *Barleria*, *Asystasia* etc. Between the altitudes of 1,000 m and 1,500 m, dense wet forests occur. The trees are tall and represented by *Hopea*, *Balanocarpus Artocarpus hirsuta*, *Bombax malabaricum* etc. *Mucuna*, *Derris*, *Hoya*, *Piper nilgirianum* etc. occur as twiners and climbers. The shrubby vegetation mainly consists of the members of the families of Acanthaceae, Rubiaceae and Leguminosae.

7.10 Alpine Vegetation : The name alpine vegetation has been derived from the flora growing between the altitudes of 3,000 and 4,000 m in the Alps mountain. Alpine vegetation consists of mostly annual and perennial plants occurring in cold regions, which not only exist in the Alps but also in the high altitudes of the mountains of tropical countries e.g. Himalayas in India. In India, the alpine habitat and flora occur in Himalayas between the altitudes of 3,500 and 5,000 m.

There are four main ecological factors operating on the alpine vegetation, these are :—(a) action of cold wind which has dry action, (b) moisture in the form of rain, dew or snowfall, (c) low temperature which sometime reaches below 0°C and (d) differences between direct and indirect sunlight which is greater than that of plains.

In alpine annual plants, the vegetative period is very short for complete growth and propagation. The flora, everywhere in high altitude mountains resemble that of *mat vegetation* of the Alps. It consists of several associations such as (i) *Nardus stricta* association that grows on poor dry soil and often alternates with dwarf shrub-heath consisting of *Rhododendron* species ; other plants occurring here and there in this association are the species of *Potentilla*, *Vaccinium*, *Luzula*, *Festuca*, *Saussurea tridactyla*, *Trifolium alpina* etc. ; (ii) *Carex* association occurs in dry tracts and has the form of low tufted plants with short stiff leaves, in this association species of *Festuca* and *Saxifraga* occur along with *Carex* species, and (iii) *Polygonum-Urtica* association—this association is composed of several species of *Polygonum*, *Rheum* and *Urtica*.

Indian alpine flora is composed of many plants which are also found in the alpine region of Europe, besides there are many central Asian, Tibetan and Japanese elements occurring in the alpine belt of the Himalayas. Himalayan alpine habitats are marked by glaciers and glacial deposits. In W. Himalayas the alpine meadow, composed of alpine mat vegetation, is located between the altitudes of 4,200 m and 4,500 m ; the flora chiefly consists of herbaceous angiosperms, lichens and mosses. At the altitude of 3,500 m species of *Juniperus* and shrubby *Rhododendron* constitute 'elfin scrub' formation. Among trees and bushes, the common plants in the alpine Himalayas are *Abies spectabilis*, species of *Juniperus* and *Rhododendron*.

The perennials are represented by the members of the families of Ranunculaceae, Cruciferae, Rosaceae, Caryophyllaceae etc.

In Sikkim Himalayas, alpine zone begins from the altitude above 3,500 m, it presents two types of climates viz. outer humid and inner dry. The dominant angiospermic families in the outer humid region are represented by Ranunculaceae, Cruciferae, Papaveraceae, Caryophyllaceae, Scrophulariaceae, Compositae, Cyperaceae and Gramineae. The main bushes consists of *Rhododendron*, species of *Juniperus*, *Ephedra*, *Berberis*, *Lonicera*, *Rosa*, *Cotoneaster*, *Spiraea* and several species of *Arenaria*. In the drier inner region, species of *Arenaria*,

Meconopsis, *Rheum*, *Saussurea* etc. are found. According to Smith, the arboreal alpine vegetation of S. E. Sikkim above 3,500 m comprises mostly of *Rhododendron* and *Abies spectabilis* in addition to *Pyrus*, *Salix*, *Viburnum* etc. The family Ranunculaceae is represented by *Caltha* and *Anemone*. *Corydalis* of the family Papaveraceae is also a dominant genus in that area.

On phytogeographical basis, Puri (1960) has classified alpine vegetation of the Himalayas into (a) alpine stony desert, (b) alpine scrub and (c) alpine pasture. A little below the zone of perpetual snow, alpine stony desert occurs; the habitat is characterised by rocky slopes densely crowded with lichens and dicotyledonous plants like *Sedum*, *Androsace*, *Primula* etc. Alpine scrub vegetation occurs all over the Himalayas above the altitude of 3,000–3,500m; the limit of arboreal vegetation lies between 3,500 and 4,000 m; above this the vegetation is represented by cushion plants and prostrate low herbs. Above the scrub zone, alpine pasture with rich ground flora is met with. The peculiar feature of the plants of this zone is stunted growth, in many cases flowering shoots are replaced by vegetative shoots. Among the herbaceous species, species of *Corydalis*, *Draba*, *Anemone*, *Aquilegia*, *Aconitum* etc. are worth mentioning.

The leaves of alpine plants are provided with well developed palisade tissue, the spongy tissue has larger intercellular spaces, presence of large quantity of chloroplasts in leaves indicates their vigorous assimilation capacity. The colour of flowers is deep ranging from brilliant red, yellow to blue.

SELECTED QUESTIONS

1. What do you mean by ecology? What are its divisions?
Refer articles 1.1 and 1.3
2. Discuss briefly the aims and scope of plant ecology.
Refer article 1.2
3. Define the term vegetation. How it originates? What are the different types of life-forms of plants noted in a vegetation?
Refer chapter 2
4. What is meant by climatic factors? Name and classify several factors of the environment that influence the distribution of plants.
Refer part one, chapter 3
5. Enumerate the main ecological factors. Explain with reference to a particular locality how each of these factors affect the vegetation of the locality chosen by you.
Refer chapter 3
6. Discuss briefly how climatic factors influence the vegetation of a country. Or, Narrate the important role of the climatic factors in the distribution of plants.
Refer article 3.1
7. Describe the role of edaphic and biotic factors in the distribution of plants.
Refer articles 3.3 and 3.5
8. What are the principal ecological factors that influence vegetation? Or, Write a short essay on the ecological factors which affect plant life.
Refer articles 3.1, 3.2, 3.3 and 3.5

9. Discuss the role of light as a factor in ecological formations.
Refer article 3.1 (d).
10. Give an account of the relation between soil texture and vegetation.
Refer article 3.3 (f).
11. What are the main soil factors which control the ecological distribution and growth of various species.
Refer article 3.3
12. Discuss briefly the origin and development of soil in a particular region.
Refer article 3.4
13. What do you mean by soil profile ? How do the different soil horizons and soil strata differ from one another ?
Refer article 3.4, page 376 (paras 3 and 4)
14. What is meant by a plant community ? How does it originate in a particular area ?
Refer article 4.1 and 4.1A
15. Discuss the origin, development and succession of plant communities.
Refer articles 4.1A and 4.2A (page 387, process of succession)
16. Classify with examples different types of plant communities you have studied.
Refer article 4.1B
17. What do you mean by plant formation ? Write an essay on the origin, factors and types of plant formation with special reference to India.
Refer article 4.1, B I
18. Distinguish between plant formation, plant association, consociation, faciation and society. Give examples of each.
Refer article 4.1, B I (para one), II, III, IV and V
19. What do you mean by plant succession ? How succession develops in a particular region ? What are the causes of succession ?
Refer article 4.2 (para one) and also pages 387-388
20. Give an account of the factors leading to seasonal succession.
Refer article 4.2
21. What is meant by plant succession ? Describe the various stages of succession in xerosere.
Refer article 4.2 (para one) and page 386 (xerosere)
22. What is sere ? Describe the different stages of succession in a hydrosere.
Refer article 4.2, pages 385 and 386.
23. What are the methods of studying vegetation ? Describe them briefly.
Or, Give an account of the different methods of ecological study of vegetation in the field.
Refer article 4.3
24. Describe the vegetation of a fresh water pond and mention the ecological adaptations of the species. What are the factors which affect their distribution ?
Refer article 5.1, A - D
25. Describe with examples the various adaptations in floating plants.
Refer article 5.1, A
26. Write an illustrated account of the morphological and anatomical peculiarities of aquatic flora of West Bengal.
Refer article 5.1, A - D (adaptations only)
27. Give an account of the morphological, anatomical and physiological adaptations found in xerophytes, halophytes and hydrophytes. Give common examples from each group.
Refer article 5.13. For the examples refer name of plants under articles 5.4, 5.5 and 5.1 respectively.

28. Describe the adaptations met within mangrove plants.
Refer article 5.7, page 412 (adaptations)
29. Give an account of morphological and physiological peculiarities of mangrove plants. Or, Give an account of the ecological adaptations of mangrove plants. Give botanical names of two typical mangrove plants of Sunderbans.
Refer article 5.7, page 412
30. Give a general account of the mangrove vegetation with special reference to West Bengal.
Refer articles 5.6(A) and 5.7 (F, page 410)
Or, Give an account of the characteristic flora in the mangrove vegetation of Sunderbans. Or, Give an account of the characteristic adaptations of the flora of saline tracts of West Bengal.
Refer article 5.7 (F)
31. Give an account of the vegetation of a salt marsh citing examples to illustrate your answer.
Refer article 5.6, B
32. Give an account of the ecology of plants found in sea beach.
Refer article 5.6 (A)
33. Mention the different parts of India where mangrove vegetation is found. Describe the special physiological conditions under which these plants grow.
Refer article 5.7
34. Describe how anatomical features of a plant indicate its environment with special reference to halophytes.
Refer article 5.5
35. Describe briefly with examples the characteristic adaptations of (a) epiphytes, (b) mangroves, (c) desert plants and (d) submerged plants.
For (a) refer article 5.11; for (b) refer article 5.7 page 412, for (c) refer article 5.4 and for (d) refer article 5.1 (C)
36. Describe briefly with sketches the morphological and anatomical peculiarities of the following plants :
(a) Water lily, (b) *Vallisneria*, (c) *Nerium*, (d) *Avicennia officinalis*, (e) *Cycas*, (f) an epiphytic orchid.
Refer articles 5.1B for (a) ; 5.1C for (b) ; 5.4 for (c) ; 5.5 for (d) ; 5.4 for (e) and 5.11 for (f).
37. Refer the following plants to their habitats and explain their special structural adaptative features :— (a) orchid, (b) a typical cactus, (c) water hyacinth.
(a) refer article 5.11 ; (b) refer article 5.4 ; (c) refer article 5.1(A).
38. What do you mean by plankton ? How it differs from pleuston ? Write an essay on plankton formation with special reference to its flora and adaptations.
Refer article 5.2
39. Give the characteristics of the planktonic flora of a large neglected tank or of a swamp. Or, Give an account of the special features of the cryptogamic plankton in stagnant pools.
Refer article 5.2
40. Write a brief account on pleuston formation.
Refer article 5.3
41. Define hydrophytes, xerophytes, halophytes and lithophytes. Give at least two examples from each type.
Refer articles 5.1 (para one) ; 5.4 (para one) ; 5.5 (para one) and 5.8 (para one). For examples see name of plants under each article.

42. What do you mean by mesophytes ? Give a brief account of mesophytes with special reference to adaptations.
Refer article 5.9
43. Give an account of the common plants in a village in Bengal plains which you have studied.
Refer articles 5.1, 5.9, 5.10, 5.11 and 5.12 (vide list of plants under each)
44. Write an essay on different types of formations noted on rocky substratum with special reference to their adaptations and flora.
Refer article 5.8
45. What are lithophytes ? Discuss the morphological, histological and physiological characteristics of such plants.
Refer article 5.8
46. Give the characteristic of drought resisting plants citing known examples.
Refer article 5.4(d)
47. Describe the special ecological features of sand flora.
Refer article 7.6
48. Write an essay on the ecological adaptations of epiphytic flora.
Refer article 5.11
49. Write an essay on parasitism in plants.
Refer article 5.12
50. Give an account of the ecological features and location of a rain forest in India.
Refer article 7.1
51. Mention briefly the ecological features of forest vegetation in West Bengal. What climatic factors are responsible for evergreen forest in India ?
(For 1st part refer article 7.1 page 429 (adaptations), 7.2 (last para) and 7.4 ; for last part refer article 7.1)
52. Give an account of the desert vegetation of India.
Refer article 7.7, A
53. What do you mean by ecosystem ? Describe in brief different types of ecosystems of the world.
Refer chapter 6.
54. Write short notes on :—
 - (a) Photophilic and photophobic plants—Refer article 3.1 (d)
 - (b) Topographic factors—Refer article 3.2
 - (c) Soil profile—Refer article 3.4, page 376
 - (d) Biotic factors—Refer article 3.5
 - (e) Plant community—Refer article 4.1
 - (f) Plant formation—Refer article 4.1 (B)
 - (g) Plant association and consociation—Refer article 4.1, B (II and III)
 - (h) Ecesis—Refer article 4.1, A
 - (i) Plant consociation—Refer article 4.1, B (III)
 - (j) Plant succession—Refer article 4.2
 - (k) Climax vegetation—Refer article 4.1 A, page 380
 - (l) Hydrosere—Refer article 4.2, page 385
 - (m) Xerosere—Refer article 4.2, page 386
 - (n) Transect—Refer article 4.3, page 390
 - (o) Tropophytes—Refer article 5.10
 - (p) Mangrove—Refer article 5.6, B, page 403
 - (q) Xerophytes—Refer article 5.4
 - (r) Morphological features of plants growing in saline environments—Refer article 5.5, page 402

CHAPTER I

Introduction

Plant geography is one of the branches of Botany which deals with the spatial (*i.e.*, relating to space) relationship of plants both in the present and the past. The main aim and object of plant geography is to record and then explain the distribution of plants over the surface of the World. According to Good (1964), plant geography is closely related to Anthropology and Zoology in addition to other branches of Botany. This branch of Botany is intimately connected with plant ecology. Now-a-days plant ecology and plant geography together constitute a new and much more wider subject known as *Geo-Botany*, which comprehends all aspects of the relation between plants and the surface of the earth *i.e.*, the substratum. Plant ecology is mainly concerned with the plants' relationship to the conditions of habitat while plant geography is concerned "with the correlation between plants and the distribution of external conditions."

The distribution of various types of plants belonging to different taxa over the surface of the earth is greatly influenced by the relative position of six continental land masses, numerous islands, the vast stretches of deserts and oceans etc. The distribution of plants in different regions depends primarily upon two factors *viz.*, (a) *inherent* and (b) *geographic*. The 'inherent' factor is mainly genetical and concerned chiefly with the evolution of an individual and its immobility while the 'geographic' factor is ecological and topographical. For this, the geographic factor is again sub-divided into (1) *climatic factors* and (2) *barrier factors*. Barriers are natural obstacles of mountains, oceans, deserts etc. which cannot be crossed ordinarily by spreading species for their dispersal. Barrier factor is the main factor and is of greater significance regarding the distribution of species over the world's surface than the climatic factor. The distribution of species is also greatly influenced by *biotic factors*.

1.1 The Nature of the Division of the World into Floristic Regions : Now-a-days, the major segregation of plant-life of the world lies in three latitudinal zones *e.g.*, (a) polar, (b) temperate and (c) tropical zones. Due to the shape of the earth and its position in relation to the sun, these zones are symmetrical about the equator. Hansen (1920) has suggested a fuller and more scientific classification of world's floristic regions. He divided the earth into eight distinct zones on either side of the equator which are as follows :

1. Equatorial zone ... 0°-15° degrees on either side of equator
2. Tropical zone ... 15°-23°5' " " " " " "

- | | | |
|------------------------|---------------|-----------------------------------|
| 3. Sub-tropical zone | ... 23°5-34°0 | degrees on either side of equator |
| 4. Warm temperate zone | 34°0-45°0 | " " " " " " |
| 5. Cold temperate zone | 45°0-58°0 | " " " " " " |
| 6. Sub-arctic zone | ... 58°0-66°6 | " " " " " " |
| 7. Arctic zone | ... 66°5-72°0 | " " " " " " |
| 8. Polar zone | ... 72°0-90°0 | " " " " " " |

Hansen's classification is somewhat complicated when the influence of the evolution factor of land is taken into consideration.

The vegetational zonation of mountains, especially of tropical mountains has been studied by several botanists and which has been expressed in a number of classifications. Of all such classifications, the following is a familiar one :

0- 600 metres	...	Zone of plams and bannans
600-1,250	„	Zone of tree ferns and figs
1,250-1,900	„	Zone of Myrtales and Lauraeals
1,900-2,600	„	Zone of evergreen trees
2,600-3,200	„	Zone of deciduous trees
3,200-3,800	„	Zone of coniferous trees
3,800-4,450	„	Zone of alpine shrubs
4,450-5,050	„	Zone of alpine herbs
5,050-and above	...	Permanent ice and snow

In the tropics, 77% of the total land is occupied by tropical vegetation, 17·5% is occupied by sub-tropical vegetation, 4% by temperate and 1·5% by arctic alpine vegetation. In the sub-tropical regions only about 67·5% of the total land is occupied by sub-tropical vegetation, 17% by temperate vegetation and 9% by arctic alpine vegetation. In the temperate regions about 74% of the total land is occupied by temperate vegetation, while 18·5% is occupied by arctic alpine vegetation.

1.2 Phytogeographical Regions of the World : Several attempts have been made from time to time of a suitable classification of the phytogeographical regions of the world : of these classifications of Schouw (1928) and Good (1947, 1964) are important. Schouw divided the entire world into 25 kingdoms which he named after their most important and common plants ; kingdoms were again sub-divided into provinces which were also named after the characteristic plants of respective provinces.

On the basis of the floristic pattern, Good (1964) has divided the world into 6 kingdoms. Of these kingdoms, only one has been divided into sub-kingdoms. These kingdoms and sub-kingdoms are further divided into regions and ultimately into provinces. The outline of Good's classification is as follows :

I. BOREAL KINGDOM :

1. *Arctic and Sub-arctic Region*

- (a) Eurasian province
- (b) Greenland
- (c) Nearctic

2. *Euro-Siberian Region*A. **European Sub-region**

- (a) Western Europe
- (b) Central Europe
- (c) Scandinavia
- (d) Russia
- (e) Danube basin
- (f) European alpine
- (g) Caucasus

B. **Asiatic Sub-region**

- (h) Western Siberia
- (i) Altai-Trans Baikal
- (j) North-eastern Siberia
- (k) Kamchatka

3. *Sino-Japanese Region*

- (a) Manchuria and South-eastern Siberia
- (b) North Japan and South Sakhalia
- (c) Korea and South Japan
- (d) North China
- (e) Central China
- (f) Sino Himalayan Tibetan mountains

4. *Western and Central Asiatic Region*

- (a) Armenian-Persian Highlands
- (b) South Russia—Trans-Caspia
- (c) Turkestan and Mongolia
- (d) Tibetan plateau

5. *Mediterranean Region*

- (a) Lusitania and Western North Mediterranean coasts and islands
- (b) Eastern North Mediterranean coasts and islands
- (c) Morocco-Tunis
- (d) Libya, North Egypt and Syria

6. *Macaronesian Region*

- (a) The Azores
- (b) Madeira
- (c) The Canaries
- (d) The Cape Verdes

7. *Atlantic North American Region*A. **Northern Sub-region**

- (a) Canadian Conifer province
- (b) The Great Lakes
- (c) The Appalachians

B. Southern Sub-region

- (d) The Prairies
- (e) Atlantic and Gulf coasts
- (f) Mississippi basin

8. *Pacific North American Region*

- (a) Southern Alaska and Aleutian Islands
- (b) Sitka, British Columbia, Washington and Oregon
- (c) Californian coast
- (d) The great Basin
- (e) Rocky mountains
- (f) Sierra Nevada
- (g) Mexican Highlands

II. PALAEOTROPICAL KINGDOM :**9. *North African—Indian Desert Region***

- (a) Sahara—Arabia (except the South)
- (b) Mesopotamia—South Persia—West Pakistan

10. *Sudanese Park Steppe Region*

- (a) Senegambia—Sudan
- (b) Upper Nile-land

11. *North-east African Highland and Steppe Region*

- (a) Abyssinia and Eri
- (b) Galaland Somaliland
- (c) Yenien and South Arabia
- (d) Socotra

12. *West African Rain forest Region*

- (a) Upper Guinea
- (b) Cameroons and Islands
- (c) Congo basin

13. *East African Steppe Region*

- (a) Southern Portugese East Africa
- (b) The East African Steppness
- (c) The East African high mountains
- (d) The Central African lake zone
- (e) The Rhodesias
- (f) Angola

14. *South African Region*

- (a) High veldt of Orange Free State and Transvaal
- (b) The Kalahari
- (c) The Karroo
- (d) Namaqualand and Damaraland
- (e) Natal and eastern Cape Province

15. *Madagascar Region*

- (a) Madagascar and the Comoros
- (b) The Seychelles
- (c) The Mascarenes

16. *Region of Ascension and St. Helena*

- (a) South China and Hainan
- (b) Formosa and the Riukin Islands
- (c) Siam and Indo-China

B. Indo-Malaysian Sub-kingdom**17. *Indian Region***

- (a) Ceylon
- (b) Malabar coast and Southern India
- (c) Deccan
- (d) Ganges Plain
- (e) Flanks of the Himalayas

18. *Continental South-east Asiatic Region*

- (a) Eastern Assam and Upper Burma
- (b) Lower Burma

19. *Malaysian Region*

- (a) The Malay Peninsula
- (b) Java, Sumatra and Sunda Islands
- (c) Borneo
- (d) Philippines
- (e) Celebes and Moluccas
- (f) New Guinea and Aru

C. Polynesian Sub-kingdom**20. *Hawaiian Region*****21. *Region of New Caledonia (with Lord Howe and Norfolk Islands)*****22. *Region of Melanesia and Micronesia*****23. *Region of Polynesia.*****III. NEOTROPICAL KINGDOM :****24. *Caribbean Region***

- (a) Mexican lowlands and coast
- (b) South Florida, West Indies, Bahamas, Bermudas
- (c) Guatemala-Panama
- (d) North Colombia and North Venezuela

25. *Region of Venezuela and Guiana*

- (a) Orinoco Basin
- (b) Uplands of Venezuela

26. *Amazon Region*

27. *South Brazilian Region*
 - (a) Eastern coast
 - (b) Uplands of Central Brazil
 - (c) Highlands of Eastern Brazil
 - (d) Grand Chaco
28. *Andean Region*
 - (a) Flanks of the Andes
 - (b) Montane Andes
 - (c) The Galapagos Islands
 - (d) Atacama Desert
 - (e) Chilean sclerophyll zone
29. *Pampas Region*
 - (a) Uruguay and South-eastern Brazil
 - (b) Argentine Pampas
 - (c) Western Argentina
30. *Region of Juan Fernandez*
- IV. SOUTH AFRICAN KINGDOM :
31. *Cape Region*
- V. AUSTRALIAN KINGDOM :
32. *North and East Australian Region*
 - (a) Northern forests
 - (b) Queensland forests
 - (c) South-eastern forests
 - (d) Tasmania
33. *South-west Australian Region*
34. *Central Australian Region*
 - (a) North and East Savannas
 - (b) Central deserts
 - (c) South Australia
- VI. ANTARTIC KINGDOM :
35. *New Zealand Region*
 - (a) North Island
 - (b) South Island
 - (c) New Zealand Alps
 - (d) Kermadec Islands
 - (e) Chatham Islands
 - (f) Auckland & Campbell Islands
36. *Patagonian Region*
 - (a) Patagonian and Fuegia
 - (b) Southern Andes
 - (c) Falkland Islands
37. *Region of the South Temperate Oceanic Islands*

CHAPTER 2

Phytogeographical Regions of India

On the basis of the distribution of different floristic elements in different regions of India, both British India and the present partitioned India have been divided in several phytogeographical regions by many botanists since the time of Sir J. D. Hooker.

J. D. Hooker in his "*Introductory Essays to the Flora Indica*" (1855) and subsequently in the "*Imperial-Gazetter of India*"—*Botany section* (1907), divided British India into nine phytogeographical regions as follows :—

(1) *Eastern Himalaya*, extending from Sikkim to Mishmi hills in upper Assam.

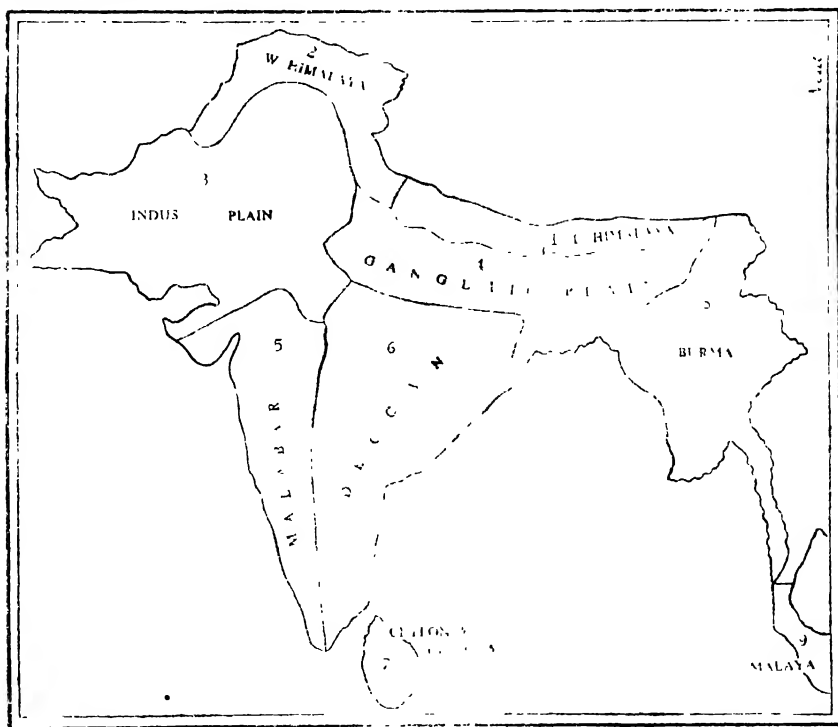


Fig. 2.1 Phytogeographical regions of British India
(after J. D. Hooker, 1907)

(2) *Western Himalaya* which cover mountainous regions from Kumaon to Chitral.

(3) *Indus Plain*—covering the Punjab, Sind, Rajputana lying to the West of Aravalli mountains and the Jumna, Cutch and northern Gujrat.

(4) *Gangetic Plain*, it includes the tracts of land from the Aravalli range and the Jumna to Bengal including Sunderbans and the plains of Sylhet, Assam and the low lying land of Orissa, North of Mahanadi. This region may be further sub-divided into three regions, e.g.

(a) an upper dry, (b) a lower humid and (c) the Sunderbans.

(5) *Malabar*, it includes the humid, hilly belt of the country extending from southern Gujrat to Cape Comorin and the Laccadive Islands.

(6) *The Deccan*, consisting of dry, elevated plateau East of Malabar and South of the Indus and the Gangetic Plains together with the Coromandelian stripe of coast land.

(7) *Ceylon and the Maldive Islands*.

(8) *Burma*.

(9) *The Malay Peninsula*.

In 1898, C. B. Clarke in the "*Journal of Linnaean Society*" proposed a somewhat different classification of Indian floral regions. His classification was based on a more statistical way and following the distribution of Cyperaceae in India. Clarke divided British India into eleven botanical regions or sub-areas which are as follows :—

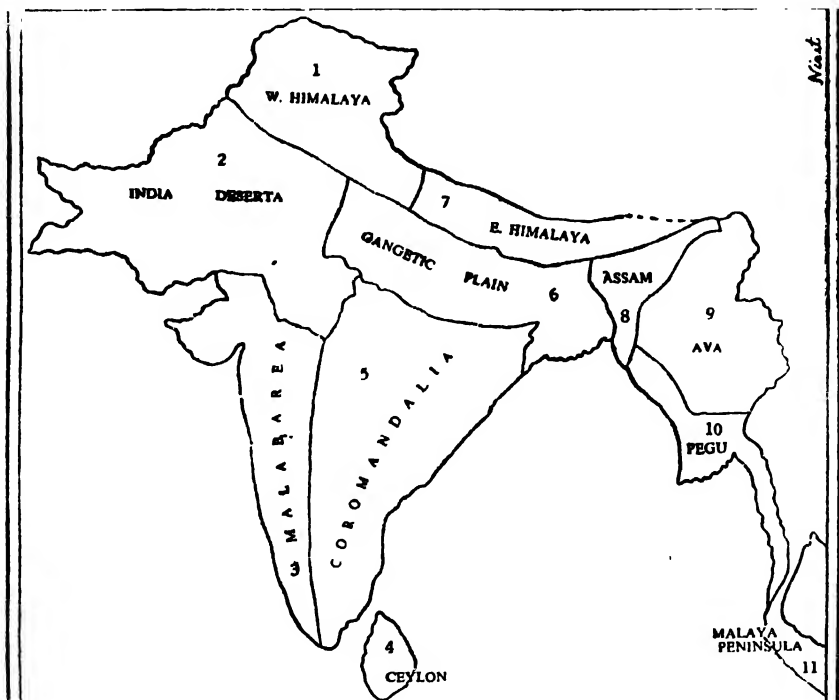


Fig. 2.2 Phytogeographical regions of British India
(after C. B. Clarke, 1898)

(1) *Western Himalaya*—Includes regions more or less like that of Hooker.

(2) *India deserta* (Indian deserts)—It includes the mountains of eastern Afghanistan, the whole of Baluchistan, South-eastern Rajputana and Central India in the region of Indus Plains of Hooker.

(3) *Malabar*a—It includes regions like that of Hooker.

(4) *Ceylon*.

(5) *Coromandalia*, corresponding to the Deccan of Hooker and others.

(6) *Gangetic Plain*—It includes region like that of Hooker excluding regions of Assam. According to Clarke, Assam forms a distinct and separate region or sub-area.

(7) *Eastern Himalaya*—It includes central Nepal and other regions like that of Hooker.

(8) *Assam*.

(9) *Ava*, it constitutes a separate region or sub-area ; Ava includes regions of northern and North-eastern Burma.

(10) *Pegu* is another distinct sub-area of Burma, it is composed of southern Burma.

(11) *Malay Peninsula*.

On the basis of climatic and physical conditions, floral features etc., C. C. Calder (1937) divided British India into six botanical regions, those regions are :—

(1) *North-Western Himalayas*—It includes regions like those of C. B. Clarke's W. Himalayan regions. Botanical province of this region consists of three altitudinal zones viz., tropical, temperate and alpine.

(2) *Eastern Himalaya*—It includes Sikkim and Upper Assam. Like N. W. Himalayas it is also divided into three altitudinal zones.

(3) *The Indus Plain*—This province includes the Punjab, Sind and Rajputana, West of Aravalli range and Jumna river, Cutch and Gujrat.

(4) *Gangetic Plain*—It includes all parts of the country drained by the Ganges and its tributaries from the edge of the elevated parts (North-west of Delhi) roughly to a North-south line running to Benaras.

(5) *Deccan*—The whole of the peninsula South of the Ganges valley and East of the Malabar Ghats is characterised by a plateau of medium height ; from this plateau rises in a West-east direction spurs from the western Ghats and through which flow eastward a series of rivers (the Godavari, Krishna, Cavery and others) draining into the Bay of Bengal. In the East, the plateau terminates in a lower range of hills (the eastern Ghats), as the land from here to sea differs from that of the Deccan in floristic elements—so this region is called coromandal sub-province (5a in Fig. 2.3).

(6) *Malabar*—It includes mountains of western Ghats.

D. Chatterjee in the “*Studies on Endemic Flora of India and Burma*” in 1939, divided the then British India into eight (10 ?)¹ phytogeographical regions which are as follows :—

(1) *The Deccan*—comprising the major parts of Madras, Hyderabad and Mysore.

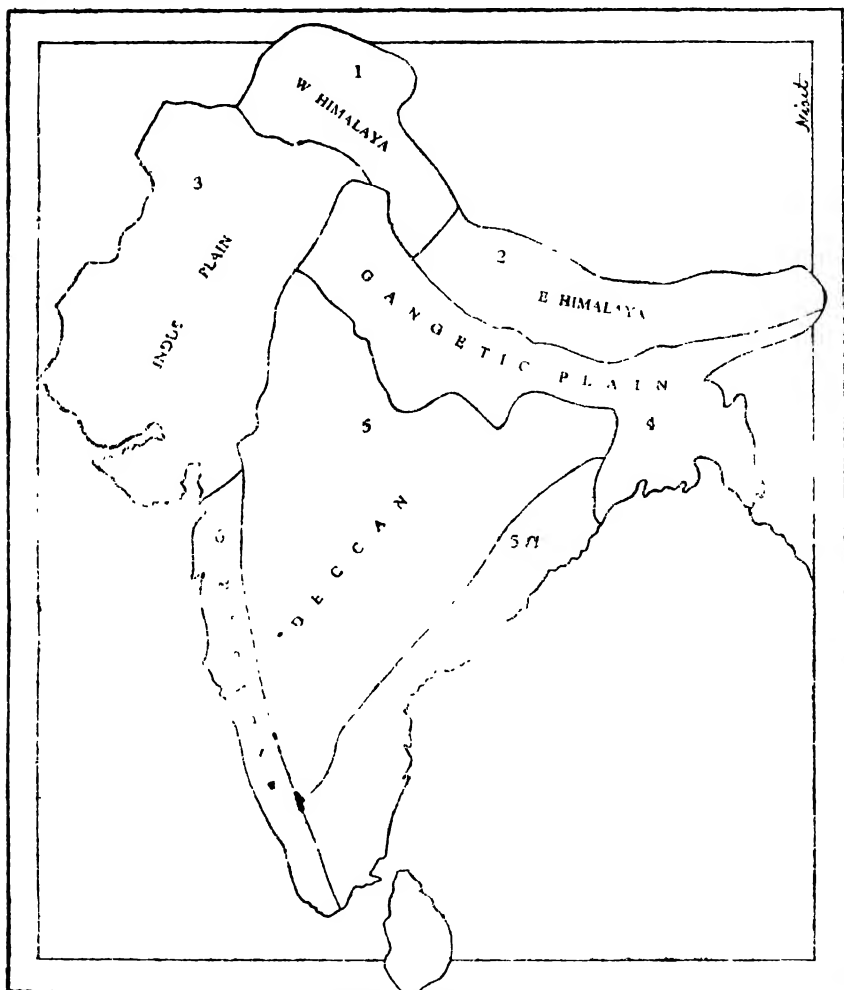


Fig. 2.3 Phytogeographical regions of British India (after C. C. Calder, 1937)

¹ Though D. Chatterjee (1939) has shown two more regions viz., Upper Burma (9) and Lower Burma (10) in his proposed table and Map (*Journ. Royal Asia Soc. Beng. Sci.* 5 : pages 24 and 25) but in the text he has neither mentioned nor explained anything about those two regions ; instead he has clearly mentioned his

(2) *Malabar*—consisting of the major parts of Bombay Presidency and the Travancore State.

(3) *The Indus Plain*—This region is sub-divided into dry desert region of Sind, Rajputana and part of Baluchistan and the humid region of the Punjab.

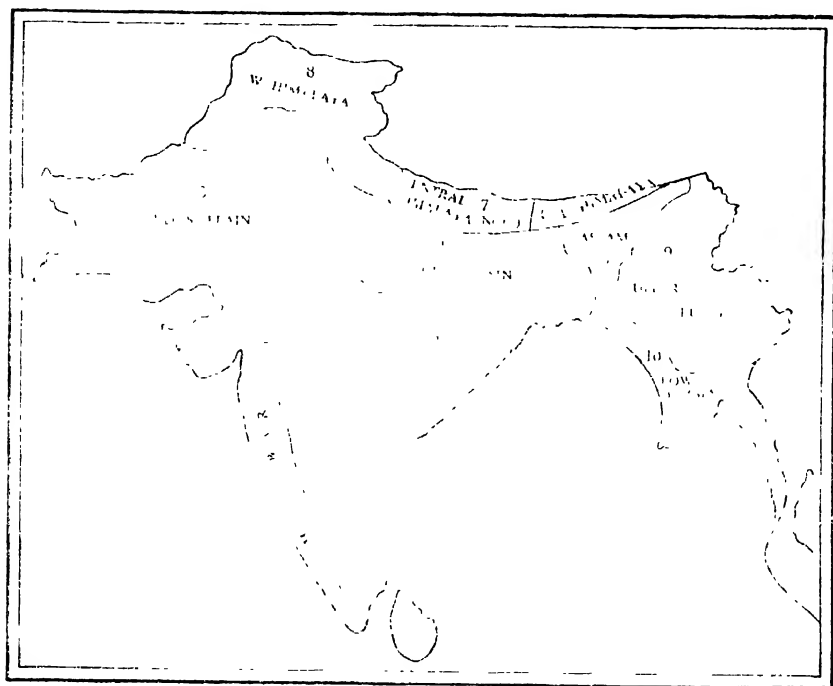


Fig. 2.4 Phytogeographical regions of British India (after D. Chatterjee, 1939)

(4) *The Gangetic Plain* with an upper dry region extending from the Punjab over the greater part of the United Provinces as far east to Allahabad, and lower humid region including the rest of the United Provinces, Behar, Orissa and Bengal excepting the areas in the Gangetic delta.

(5) *Assam*.

(6) *Eastern Himalaya*—including Darjeeling district of Bengal, Sikkim, Bhutan and regions extending to the Mishmi hills.

(7) *Central Himalaya*—Nepal.

(8) *Western Himalaya*—extending from the Kumaon hills through Kashmere to the North-West-Frontier Province.

eight phytogeographical regions (i.e., pages 21 and 23) without putting any comment regarding exclusion or inclusion of Upper and Lower Burma as shown in his table and Map (Fig 2.4)

Ceylon and Malaya have been excluded from phytogeographical divisions of India by Chatterjee, as according to him those regions have flora which are distinctly foreign to those of India.

After the political partition of the sub-continent of British India into Indian Dominion and Pakistan, Chatterjee (1960) has suggested a revised scheme of the phytogeographical regions of Indian Dominion. In this scheme, he has shown only *eight* distinct botanical regions of India proper excluding Burma (with Upper and Lower) and the regions under both western and eastern Pakistan (Fig. 2.5). The names of the eight regions remain as it is like that of his former classification in 1939; the modifications of areas regarding exclusion from Pakistan in the phytogeographical regions are as follows :—

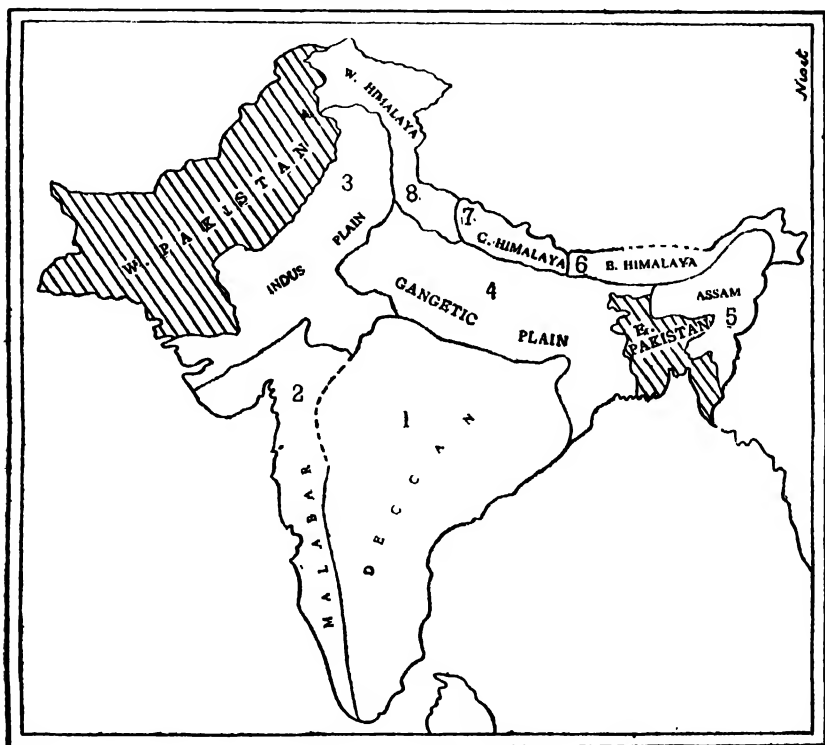


Fig.2.5 Phytogeographical regions of India after partition (after D. Chatterjee, 1960)

The *Indus Plain* now consists mainly of Rajasthan (*i.e.*, dry deserts of former Rajputana), the humid regions of Punjab and Himachal Pradesh.

The *Western Himalaya* contains the regions *excluding* the North-West-Frontier Province which is now under Western Pakistan.

From the *Gangetic Plain*, eastern part of Bengal and the major portion of the Sunderbans (now forming E. Pakistan) are excluded.

Table showing phytogeographical regions of India (before and after political partition) proposed by Clarke (1898), Hooker (1907), Calder (1937) and Chatterjee (1939, 1960). The numbers before the name of each region indicate the sequences followed by respective authors, which are also retained in maps (vide figs. 2.1-2.5)

C. B. Clarke (1898)	J. D. Hooker (1907)	C. C. Calder (1937)	D. Chatterjee (1939)	D. Chatterjee (1960)
1. West Himalaya	2. Western Himalaya	1. North West Himalaya	8. Western Himalaya	8. W. Himalaya
2. India Deserta	3. Indus Plain	3. Indus Plain	3. Indus Plain	3. Indus Plain
3. Malabar	5. Malabar	6. Malabar	2. Malabar	2. Malabar
4. Ceylon	7. Ceylon & Maldives
5. Coromandalia	6. Deccan	5. Deccan	1. Deccan	1. Deccan
6. Gangetic Plain	4. Gangetic Plain	4. Gangetic Plain	4. Gangetic Plain	4. Gangetic Plain
7. East Himalaya	1. Eastern Himalaya	2. Eastern Himalaya	6. Eastern Himalaya	6. E. Himalaya
8. Assam	5. Assam	5. Assam
.....	7. Central Himalaya	7. Central Himalaya
9. Aya	8. Burma	9. Upper Burma
10. Pegu	10. Lower Burma
11. Malaya Peninsula	9. Malaya Peninsula

Endemism is the phenomenon of the confinement of species, genera or other groups to a small area beyond which their existence is not found. Now-a-days, species confined to large areas are also regarded as endemics.

3.1 Theories on Endemism : The cause of endemism or the endemic state of a species or a genus has been explained variously. According to the view of Ridley (1922), endemic species and genera are the survivals of the larger groups of the past (relic type) which are now in course of gradual extinction. According to him, the survivals, (i.e., surviving species) are *epibiotics* i.e., they do not spread but remain as relics of the past in an isolated area which, due to some reason, has not been overwhelmed by later invading flora. These survivals are not provided with suitable and enough means of dispersal, so that they are unable to cross the barrier of recent flora and to reach another area for their establishment—hence they become confined to a limited area. On the other hand, Willis (1922) holds that endemic species and genera are *new and recent* forms of gradually extending plant-groups and they represent juvenile forms in course of spread and expanse—this theory is based on ‘age and area’ hypothesis of Willis. According to this hypothesis, the occurrence of diverse species and genera in a particular place is proportional to the age in the evolution. So a small area containing definite plant-groups where they are endemic indicates their relatively recent age. Willis also suggests that all endemic species occupying a small area are to be regarded as younger species but this view has been criticised by Chatterjee (1939) on the basis of the idea that the fact may “be correct for a larger number of species but certainly not for all”.

Supporters of the former i.e. ‘epibiotic’ theory put forward examples of tree ferns, *Metasequoia*, *Ginkgo biloba* etc. which are relic species and endemic in China and Japan. Supporters of the second theory, who hold that endemic flora are recent, cite examples like numerous species of *Primula*, *Impatiens*, *Gentiana*, *Rhododendron* etc. which are endemic in particular areas.

From the above two ideas proposed by two different schools, Chatterjee puts his opinion “that both schools are correct in their views, but from the evidence of large number of new forms, continually arising by natural crossing and mutation, it is quite likely that the latter view has more supporters”.

Chatterjee also holds that the distribution of endemic species indicates their age. Supporting Willis’ idea, he also emphasised that the frequency of species over an area varies directly with its age in evolution—this statement has been further supplemented by him by the following figures of endemic species from old i.e. British Indian areas :—

Number of endemic species common generally in India.....	533
Number of endemic species in Himalayas only	3,165
" " " " " Continental India	2,045
" " " " " Burma.....	1,071

3.2 Factors responsible for Endemism : The main and important factors for the production of endemic species are natural crossing and mutations among the closely related plants growing in a favourable locality. This effect may further be enhanced by the removal of

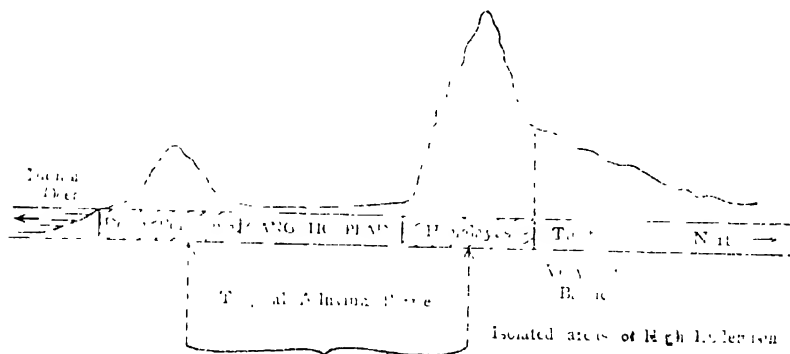


Fig. 3.1 Figure showing the influence of barriers in the induction of endemism in South India and the Himalayas (after D. Chatterjee, 1939).

external influence i.e., by the creation of a state of *isolation*, e.g., the vegetation of oceanic islands consists of many endemic species such as 82% of the species in Hawaii islands are endemic, 72% in New Zealand and 50% in Fiji islands. Isolation is the main factor which also causes endemism in many parts of continental areas; the most common forms of isolation are either lofty mountainous chains or very dry regions i.e., deserts etc. separating two land areas. In India, typical example is noted in the Himalayan range which contains high percentage of endemic species. Himalayan range has the warm alluvial plains of India to the South and the dry Tibetan plateau to the North, consequently species composing the temperate and alpine vegetation of the Himalayas have *freely formed* new species (by natural crossings and mutations among themselves) within this area. South India also contains large number of endemic species while Indo-Gangetic plain is comparatively poor in endemic species.

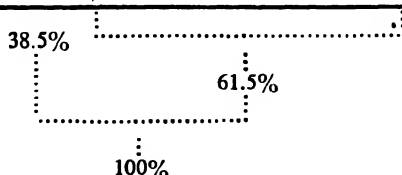
All such endemic species are unable to migrate freely, either to the North or to the South due to natural and physical barriers of lofty mountain chains in the North and ocean in the South.

3.3 Endemism in India and Burma : As India is surrounded by widely separated countries and is a part of the large continent, so there is great diversity in opinion whether India has a characteristic flora of her own or not ; this diversity in opinion is due to the richness and great variation of plants in India. According to Hooker (1904) and Champion and Trevor (1938), the flora of India is a mixture of flora of the surrounding countries like Malaya, Orient, Africa, Tibet, China and Japan. But Chatterjee (1960) from his critical studies on Indian vegetation concluded that "India has a flora of her own" because India has not only a rich endemic flora but also a larger number of endemic species.

According to the estimation of Chatterjee (1939), total number of dicotyledonous species in India is 11,124 (approx.), of which 61.5% of the plants are endemic in British India i.e. India including Pakistan and Burma ; the rest 38.5% of the total plants occur as 'wides' i.e. they are also found in other countries. British India had three regions viz. (a) the Himalayas, (b) the Indian Peninsula forming 'Continental India' and (c) Burma which contained large number of endemic species and thus those regions jointly contributed to the high percentage of endemic species ; the endemic percentage of each of those regions, if calculated separately, will however range from 50%-70%, if not more in the Himalayan region. Other parts of India viz. the Indo-Gangetic Plains and the desert regions of Sind, Rajasthan and dry regions of Baluchistan are very poor in endemic species.

The total number of dicot species recorded from British India with the number of 'wides' and proportion of endemic species in different regions is shown in the following table (after Chatterjee, 1939) :—

Total No. of dicot species	Total No. of genera	Wides i.e. found in other countries	Endemics			
			Continental India	Himalayas with Assam	Burma	General area
11,124	1,831	4,274	2,045	3,169	1,071	53.0
Percentage	...	38.5	18.2	28.8	9.6	4.9



In 1960, Chatterjee has shown that partitioned India (i.e., India excluding Pakistan, Burma and Ceylon) contains more than 50% of the dicotyledonous species as endemic. These endemic species are largely concentrated in two regions, viz. (a) the Himalayas and

(b) South India. The Indo-Gangetic Plain is comparatively poor in endemic species. The development of such a large number of endemic species is mainly due to the unique geographical features of India, and natural and physical barriers of lofty mountain chains in the North and ocean in the South (Fig. 3.1).

The highest number of endemic genera is found in the families of Papilionaceae, Rubiaceae, Gesneriaceae, Compositae, Asclepiadaceae, Euphorbiaceae, Acanthaceae, Primulaceae, Balsaminaceae, Rosaceae etc.

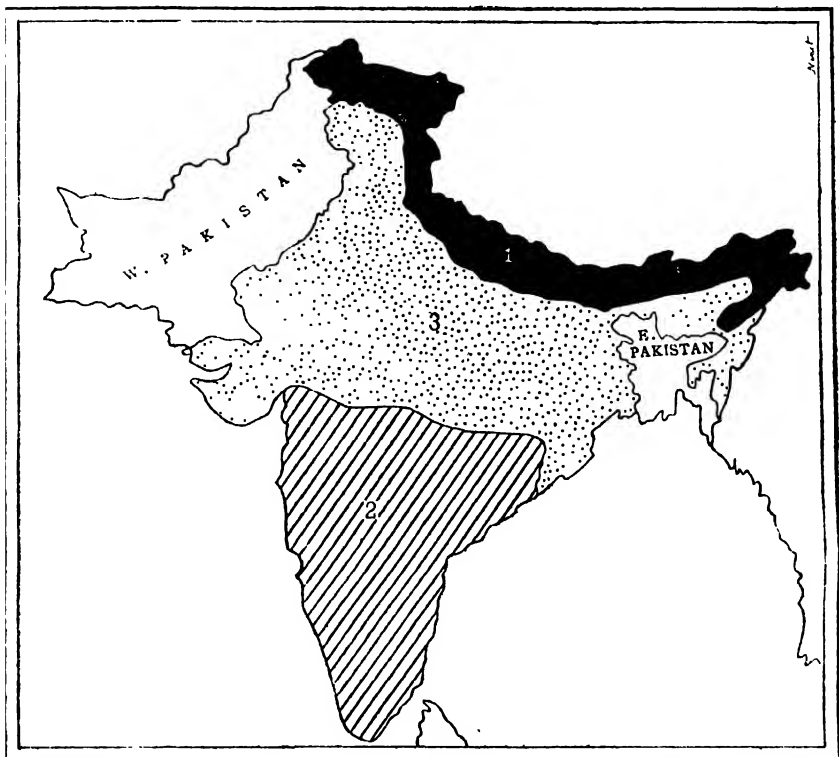


Fig. 3'2 Map showing areas of endemic plants in Himalayas (1), Peninsular India (2) and Indo-Gangetic Plain (3). After Chatterjee, 1960.

Members of the family Ranunculaceae are mostly confined to the Himalayas, Upper Burma and the temperate hilly regions of South India; the percentage of certain ranunculaceous genera is as follows :—*Ranunculus*—36%, *Clematis*—76%, *Thalictrum*—79%, *Delphinium*—71%, and *Aconitum*—90%. The endemic species of the family Cruciferae are restricted in western Himalaya and the drier parts of N. W. India; eastern Himalaya and the plains of India contain a few endemic species—the total endemic percentage is 56 only. Of the two genera viz. *Impatiens* and *Hydrocera* belonging to the family Balsaminaceae, *Impatiens* show large number of endemic

species (220 out of 241, thus the endemic percentage is 91) confined to the humid eastern Himalaya, Burma, South India and Ceylon, whereas species of *Impatiens* are totally absent in the intermediate regions of Indus Plain and Gangetic Plain—this shows that both Himalayan and South Indian regions must have been separated from each other for a long time and have developed parallel, each producing its own type of endemic species. Papilionaceae contains large number of species e.g., 867, of which 495 are endemic and 372 are wides—the endemic percentage is 57; *Dalbergia* species are found in Himalayas. *Crotalaria* and *Tephrosia* have greatest development in South India, *Milletia* has got largest number of endemic species (16) in Assam and Burma, *Caragana* and *Astragalus* have endemic species in dry western Himalaya. The endemic percentage of the family Rosaceae is 70, total number of species is 257 of which 179 are endemic. Most of the species are confined to the alpine Himalayan regions. Rubiaceae, one of the largest dicot families, is well represented in Continental India, Burma, Assam and sub-temperate regions of the Himalayas; in India there are 551 species, of which 364 are endemic and 187 are wides—thus endemic percentage is 67. Of the family Rubiaceae, following six genera are entirely endemic in India:—*Clarkella* (W. Himalaya), *Polyura* (Khasia, E. Himalaya), *Parophiorrhiza* (Khasia), *Carlemannia* (Khasia, E. Himalaya), *Silvianthus* (Khasia) and *Octotropis* (S. India). The family Compositae, though a dominant and largest types of Indian flora but has only 52% endemic species; this is due to the 'wides' condition of about half of the total number of species; the distribution of endemic species ranges from tropical regions to high alpine. Genera *Aster*, *Anaphalis*, *Centratherum* and *Vernonia* contain maximum endemic species. The genus *Rhododendron* of the family Ericaceae contains 126 species, they are abundant in the eastern Himalaya and also in North Burma; they extend also to N. W. Himalayas to Khasia and even to the Nilgiris in the South. The number of endemic species in Himalayas is 64 and in Upper Burma 44—this figure gives a high endemic ratio of 90%.

The genus *Primula* of the family Primulaceae contains 162 species mainly confined to eastern Himalaya—of these 162 species, 148 are endemic and thus endemic percentage is 91. Family Asclepiadaceae contains 234 species, of which 172 are endemic which brings the endemic percentage to 73%. Most of the species are confined to the Deccan Peninsula and the foot hills of the Himalayas. In India large number of species of the family Acanthaceae occurs in the tropical and sub-tropical regions—they are abundant in Deccan Peninsula where more than 188 species are endemic; the general endemic percentage of the family is 82. The highest endemicity is seen in the genus *Strobilanthes* where, out of 152 species, 146 species are endemic. *Stenosiphonium* contains all species (5) endemic to S. India. In India, the family Euphorbiaceae has moderate endemicity, only 63%; the main concentration of species is found in warm and dry localities of Deccan Peninsula, few endemic species are also found in Himalayas and Burma; but in India proper, out of 70 genera only 5 are endemic. The genus *Euphorbia* shows 41 endemic species out of total 63.

Vegetation Types of India

India, in its floristic composition represents a miniature world as India has varied ecological types of vegetation such as tropical, sub-tropical, temperate and alpine with varied habitat characters like mesophytes, hydrophytes, halophytes and xerophytes. The term India as used herein excludes Burma, Ceylon, Bangladesh and Pakistan.

India probably represents a greater variety of meteorological conditions. Rainfall is associated with the humidity of the atmosphere which exercises a great influence on vegetation. Rainfall varies from about 1,138.5 cm in the hills of Assam and to the North-east of the Bay of Bengal and from 885.0 cm in some parts of western Ghats to as little as 7.6 cm per annum in Rajasthan. Temperature which has considerably less importance to plant life than water supply, also exerts great influence in the formation of vegetation, specially in the high altitudinal Himalayan range.

The topography of India i.e. physical features comes second in its importance to the formation of vegetation, this is only due to the influence of variable climatic conditions. In the North, extending from Assam to Kashmir, there lies a massive range of Himalayas with a richer and more varied types of vegetation than that of any other parts of India. Himalayan range is separated from Peninsular India by the Indo-Gangetic depression, it is a broad belt of country where greatest extreme conditions are found for plant life. India, south of the depression is characterised by mountains in the West running parallel to the coast, on the North by the Aravalli range and the elevated uplands of Madhya Pradesh and Chota-Nagpur and on the East by eastern Ghat range.

The dicotyledonous plants are represented by more than 11,500 species covering about 1,800 genera belonging to 140 families of angiosperms. The monocotyledons are represented by 35 families, the number of species is about $\frac{1}{3}$ rd of the dicotyledonous species. India has percentage of endemic flora, about 50% of the total flora is endemic. Of the elements of the flora of India, the Malayan is dominant. Due to sea as more effective barrier, the African, Australian and American elements are less well represented than the European and middle East flora. According to Calder (1937) not less than 570 European genera are present in Indian flora, most of them are monotypic. The Australian element in the Indian flora is curiously represented by certain species of genera which are all but endemic in the southern continent, e.g., *Leptospermum*, *Melaleuca*, *Stylidium*, *Casuarina* etc. In some places Indian landscapes are characterised by few assemblages of plants e.g., *Rhododendron* belt in Himalayas,

the Pines of North west, bamboos in some parts of South India, xerophytic vegetation of the Indian deserts etc.; again Indian vegetation over considerable areas is marked by few dominant plant groups e.g., Palms in the lower areas of the Peninsula, *Strobilanthes* in Nilgiris, *Dipterocarpus* in the extreme East of India and Burma, *Shorea robusta* (Sal) at the base of eastern Himalayas etc.

4.1 Flora or Vegetation of Western Himalayas : The western Himalayas include all the hilly regions ranging from Kumaon to Kashmir (excluding N. W. Frontier Province) and also western part of Tibet which extends from the Indus to the region of the holy lakes Manasarobar and Rakastal. The main Himalayan range is divided into three more or less parallel ranges, viz., (a) outer, (b) middle and (c) inner; of these, the outer is the lowest and inner the highest. The inner and the middle are mostly separated by the Chandrabhaga valley, and the middle and the outer by the Ravi valley. The precipitation is extremely small. The rainfall per annum (including the winter snowfall) in the Chandrabhaga valley is 15.2 cm while in the Ravi valley and at Nagar in Kulu (Beas valley) in similar situation is 121.5 cm. In outer Himalayan regions, rainfall is something between 126.0-253.0 cm per annum. Snowfall is of universal occurrence during winter. The climate is dry and cool, strong wind usually blows in the afternoon. The minimum temperature is exceedingly low; in many places, even in summer, water freezes at night and in winter the temperature falls very low indeed.

The vegetation of W. Himalayas may be divided into three altitudinal zones viz., (a) tropical and sub-tropical (up to 1,500 m), (b) temperate (situated between 2,000 and 3,500 m) and (c) alpine (begins from 4,000 m up to the level just below the snow line). The two sides of the Himalayas exhibit vegetation of extremely different types on the two sides. On the southern slope, there are luxuriant forests with all the usual accompaniments of other forms of vegetation whereas northern side is practically a barren desert (Kashyap, 1925). The luxuriance of vegetation on Indian side gradually decreases from East to the West, this is due to some conditions like (a) gradual decrease in rainfall, (b) peculiar course of the Himalayan range from South-east to North-west and therefore the position of western part in a higher latitude and (c) great distance of western part from the sea.

The vertical sequence of vegetation in the Garhwal Himalayas (i.e., in Kumaon range) is very noteworthy. At the foot of the outer hills i.e. in tropical and sub-tropical zones, the vegetation is of sclerophyllous type; a little higher, between sub-tropical and temperate zones (609.5-1,829 m) forests of *Pinus longifolia* are met with and which gradually becomes mixed with *Quercus incana*; still higher other oaks e.g., *Q. semecarpifolia* and *Q. dilatata* with *Cedrus deodara*, *Pinus excelsa*, *Picea morinda*, *Abies pindrow* and higher up *A. webbiana* are met with. In temperate zone, species of oaks (i.e., *Quercus*) occur with the association of some deciduous trees like *Acer*, *Alnus*, *Aesculus*, *Betula* and two species of *Rhododendron*. In the inner drier valleys

like upper Sutlej (Kunawar) and upper Chandrabhaga valleys (Lahoul, Pangi and Padar), the forests are formed by *Pinus gerardiana* and *Cedrus deodara*—these trees extend to about 3,048 m or so. Still higher up in these valleys, forests of *Juniperus religiosa* and *Betula utilis* (Bhojpatra) are noted. In the tropical and sub-tropical zones comprising the Siwaliks, the main forest is *Shorea robusta* interrupted by patches of savannah, riverain types of forests and swamps. In savannahs, the arboreal plants in the grasslands are represented by *Bombax malabaricum*, *Butea monosperma*, *Acacia catechu*, *Dalbergia sisso* etc. Swampy areas contain *Cedrela toona*, *Bischofia*, *Albizia* spp. *Ficus glomerata* etc.

In the Western Himalayas, at lower levels, rich undergrowth of herbs is noted in the eastern part but towards the western part this undergrowth becomes less luxuriant. In the eastern part (in the Kali valley near Askot along Nepal borders) many epiphytic orchids and epiphytic ferns occur; at Dehradun (609·5 m) epiphytic orchids and ferns are seen while at Mussoorie and Simla (1,524-1,829 m) terrestrial orchids and ferns are found instead of epiphytic types. In the drier inner parts of Chandrabhaga and Sutlej these are absent. Besides, *Fraxinus xanthoxyloides*, spp. of *Buxus* and *Pinus* are also found.

Above the tree limit i.e., alpine zone, the vegetation is mainly grassland. The hard-rocky hills are bare and have very little water, these are covered with grass extending to the snow line. Many herbs with beautiful flowers are met with in the grass, such as species of *Anemone*, *Geranium*, species belonging to the family Gentianaceae, species of *Saussurea* with tufted habits etc. Among the gymnosperms, *Abies spectabilis*, *Picea smithiana*, *Juniperus* with association of *Betula* and *Rhododendron* are mainly found.

In the river valleys which cross the Himalayas, the vegetation gradually passes into xerophytic forms, this type is noted in Sutlej valley.

Once across the Himalayas the vegetation is changed entirely. Trees are absent except few species of *Salix* and *Populus*. In Ladak, stunted trees of *Juniperus religiosa* occur. The most important and conspicuous character of the vegetation is the cushion-like habit of all shrubby plants; *Caragana pygmaea* is such type of plant occurring as hemispherical cushions. Other species, generally found are *Arenaria polytrichoides*, *A. musciformis*, *Acantholimon lycopodioides* (Plantaginaceae); species of *Astragalus*, *Capparis leucophylla* (Capparidaceae), *Ephedra vulgaris* etc.

4.2 Vegetation of Eastern Himalayas : The eastern Himalayas include Darjeeling district of W. Bengal, Sikkim, Bhutan and regions extending to Mishmi hills in Upper Assam. Eastern Himalayan regions are bound on the north by Tibet and on the south by Bengal and Lower Assam. These regions are distinguished from western Himalayas by higher rainfall, scanty snowfall, higher humidity and

temperature. Sikkim is the most humid region and the best botanically known part of the entire eastern Himalayas.

The vegetation of this region mainly differs from that of the western Himalayas in the occurrence of more broad-leaved forests and conifers. The species of *Rhododendron* (Ericaceae) are much more in number than of W. Himalayas. The ratio of monocotyledonous plants to dicotyledonous plants is 1 : 2.5. The dominant families of angiosperms are Orchidaceae, Gramineae, Cyperaceae, Rosaceae, Leguminosae, Compositae, Fagaceae, Magnoliaceae, Dipterocarpaceae, Urticaceae, Moraceae, Melastomaceae and Euphorbiaceae. Another important feature of the vegetation is that the tropical species ascend far into temperate and the temperate ones descend into tropical altitudinal zones.

The flora is arranged as regards relative position into four altitudinal zones such as (a) tropical, (b) sub-tropical, (c) temperate and (d) alpine. The tropical zone of eastern Himalayas is mainly composed of *Shorea robusta* or 'Sal' forests with patches of riverain mixed deciduous forests, savannahs and swamps. The temperate zones of Sikkim Himalaya are divided into upper and lower zones; the upper zone is rich in conifers and bamboos (*Arundinaria* spp.), while the alpine zone is mainly composed of *Rhododendron* and *Juniperus* species.

Forest types of E. Himalayas (excluding Upper Assam)

(1) RAIN GREEN DECIDUOUS FOREST—This forest is found in tropical and sub-tropical zones covering the northern fringe of Bengal and the Himalayan foot hills to an altitude of 700 m to 900 m. Rain green deciduous forest consists of different types of deciduous trees dominated by *Shorea robusta*. Besides, other species associated with this zone are as follows :—

Trees—*Tectona grandis*, *Adina cordifolia*, *Lagerstroemia parviflora*, *Terminalia tomentosa*, *Dillenia indica*, *Dalbergia sisso*, *Syzygium wallichii*, *Phoebe lanceolata*, *Ficus hispida*, *Semecarpus anacardium*, *Bombax malabaricum*, *Quercus lancaefolia*, *Cassia fistula*, *Malotus philippinensis*, *Litsea salicifolia*, *Randia longispina*, *Albizia* spp. etc.

Shrubs and herbs—*Mussaenda angustifolia*, *Butea minor*, *Zizyphus mauritiana*, *Clerodendron* spp., *Begonia megaptera*, *B. nepalensis*, *Blumea lacera*, *Barleria strigosa*, *Hygrophila polysperma*, *Phlogacanthus thyrsoiflorus*.

The following species are found in this zone and as well as the next higher zones.

Callicarpa arborea, *C. macrophylla*, *Eupatorium odoratum*, *Bauhinia purpurea*, *Oxoxylum indicum* etc.

Towards the South of Ghorwa (350 m altitude) following species are found—

Trees forming canopy—*Shorea robusta* (dominant), *Mallotus albus*, *Bauhinia malabarica*, *Tectona grandis*, *Lagerstroemia parviflora* etc.

Shrubs—*Leea umbraculifera*, *Clerodendron infortunatum*, *Zizyphus mauritiana*, *Cycas pectinata*, *Butea minor*, *Ficus hispida* etc.

Lianes—*Bauhinia vahlii*, *Dioscorea* spp., *Hoya* spp., *Lygodium flexuosum*, *Smilax ovalifolia* etc. Besides above mentioned plants, in this zone also occur *Duabanga sonneratioides* and *Dendrocalamus* spp. in humid soil and *Pandanus* by the side of shady streams. Most of the level ground is covered with rice and jute plants. On sunny roadsides *Zizyphus mauritiana*, *Lantana camara*, *Eupatorium odoratum* etc. form thickest vegetation.

(2) MIXED BROAD-LEAVED FOREST—This type of sub-tropical mixed broad-leaved forest occurs at an altitude of 1,500 to 1,700 m. Dominant trees of this forest are *Castanopsis indica* and *Schima wallichii*.

Besides, other species associated with this zone are :—

Trees—*Michelia kisopa*, *Albizia gamblei*, *Engelhardtia spicata*, *Erythrina varieagata*, *Ficus drupacea* var. *pubescens*, *Quercus glauca*, *Litsea oblona*, *Phoebe paniculata*, *Lindera bifaria* etc.

Shrubs and herbs—*Melastoma normale*, *Sarcococca coriacea*, *Saurauja nepaulensis*, *Mussaenda treutlei*, *Begonia* spp., *Peristrophe speciosa* and *Cassia mimosoides*.

In grazing ground, *Crotalaria* spp. are common, in open places *Eupatorium odoratum* occurs while in shady humid regions various species of *Begonia* are found to grow.

In the next higher zones, the following species are commonly found.

Alnus nepalensis, *Osbekia stellata*, *Litsea citrina*, *Maesa rugosa*, *Senecio dielsiflorus*, *Arisaema* spp., *Thunbergia coccinia*, *Justicea procumbens* var. *simplex*.

Following plants are generally observed between Tharpu and Chyangthaphu (1,200 m altitude)—

Schima wallichii, *Castanopsis indica*, *Terminalia myriocarpa*, *Embllica officinalis*, *Callicarpa arborea*, *Zizyphus incurva*, *Bauhinia purpurea*, *Mallotus philippinensis*, *Maesa rugosa*, *Rhus succedanea*, *Trichosanthes wallichiana*.

A sparse forest of *Quercus incana* is found frequently on steep, rocky and south faced slopes between altitudes 1,300 and 2,200 m.

Due to various biotic factors, the vegetation of the zone has been largely destroyed.

(3) EVERGREEN OAK FOREST—This is actually a temperate forest composed of evergreen oaks and lauraceous species, occurring in the middle elevation of mountain region between 2,500 m and 2,800 m. Following plants are found in this zone :

Photinia integrifolia, *Lindera neersiana*, *Rhododendron arboreum*, *R. lepidotum*, *Symplocos phyllocalyx*, *S. ramosissima*, *Lyonia ovalifolia*, *Vaccinium vacciniaceum*, *Acer campbellii*, *Edgeworthia gardneri*,

Mahonia napaulensis etc. Dominant species—in some places *Symplocos* spp. and *Rhododendron arboreum*, in other places *Lyonia ovalifolia* and *Mahonia napaulensis* as a secondary dominant type.

Within this zone, there are two main sub-zones e.g., (a) *Castanopsis* zone up to an altitude of 2,100–2,300 m and (b) *Quercus* zone at an altitude above 2,300 m but below 2,800 m.

Castanopsis zone is dominated by *C. hystrix*, *C. tribuloides* while *Quercus fenestrata*, *Machilus edulis*, *Cinnamomum glanduliferum*, *Actinodaphne reticulata* etc. are the subordinates.

Other associated species within this zone are as follows :—

Ficus auriculata, *Ilex insignis*, *Betula alnoides*, *Elaeocarpus ganitrus*, *Michelia doltsopa*, *Prunus napaulensis*, *Acer oblongum*, *Rubus ellipticus*, *Osbeckia sikkimensis*, *Jasminum dispersum*, *Viburnum coriaceum*, *Rhododendron griffithianum*, *Anaphalis busua*, *Dicliptera roxburghiana*.

The following species are observed at Murhay, 2,000 m altitude.

Castanopsis hystrix (dominant), *Mahonia napaulensis* (sub-dominant or subordinate), *Symplocos theaefolia*, *Potentilla fruticosa*, *Lyonia ovalifolia*, *Sarcococca wallichii* etc. On rock and tree trunks, epiphytic angiosperms, ferns and mosses are luxuriant.

In *Quercus* zone, various species of *Quercus* viz *Q. lineata*, *Q. lamellosa*, *Q. semecarpifolia*, *Lindera assamica*, *Litsea elongata*, *Ilex fragilis*, *Symplocos glomerata* etc. dominate. Other species associated with this zone are *Magnolia campbellii*, *Lindera heterophylla*, *Euonymus frigidus*, *Sorbus rhamnoides*, *Gaultheria griffithiana*, *Viburnum mullaha*, *Anaphalis margarilacca*, *Arisaema griffithii* etc.

(4) RHODODENDRON—CONIFEROUS FOREST (*Alpine forest*) :

As an individual tree *Rhododendron arboreum* is found at an altitude of 1,200 m in a mixed broad-leaved forest. The *Rhododendron* forest is found above 2,500 m altitude and continues to the timber line, sometimes it has been replaced by a coniferous forest in some places (4,000 m alt.). The lower *Rhododendron* zone is composed of *R. arboreum* var. *campbelliae*, *R. barbatum*, *R. grande*, *R. thomsonii*, *R. cinnabarium*, *R. hodgsoni* etc. Other associated species in this zone are *Prunus undulata*, *Acer pectinatum*, *Viburnum cordifolium*, *Sorbus foliolosa*, *Vaccinium nummularia*, *Primula petiolaris*, *Daphne bholua* var. *glacialis* etc.

In upper *Rhododendron* zone *R. campanulatum*, *R. campylocarpum*, *R. lanatum*, *R. wightii*, etc. dominate up to the timber line. *R. anthopogon* and *R. setosum* are found in open places along the margin of the timber line. Associated species in this zone are *Prunus rufa*, *Gaultheria pyrolloides*, *Sorbus microphylla*—these are found in shady forest. In open places species of *Primula* and *Arisaema* are chiefly found. *Cotoneaster* species are found on open mountain ridges. Epiphytic mosses and lichens are luxuriant on the trees. The constituents of the *Rhododendron* forest are explained as follows :—

(a) Between Tinjuray and Hatisar (2,900 m altitude)—

R. arboreum var. *campbelliae* (dominant), *Abies spectabilis*, *Rosa sericea*, *Lyonia ovalifolia*, *Rhododendron barbatum*, *R. lepidotum* etc.

(b) Siling Tzokupa (3,000 m altitude)—

Rhododendron falconeri (dominant), *R. hodgsoni*, *R. ciliatum*, *R. lepidotum*, *R. barbatum*, *Potentilla kleiniana*, *Rubus mutantiflorus*, *R. splendidissimus*, *Anaphalis margarilacca*, *Fragaria* species. Coniferous forest is composed of two species only e.g. *Abies spectabilis* (at an upper altitude) and *Tsuga dumosa* (at a lower altitude)—these two species are accompanied by *Rhododendron* which form the secondary layers in the forest.

Coniferous forests are as follows :—

(c) Above Ramam (2,600 m altitude)

Tsuga (pure stand)

(d) Between Ramam and Phalut (2,600-2,800 m altitude)

Tsuga mixed with *Rhododendron*

Abies with *Rhododendron* (3,100-3,600 m altitude)

(e) Between Phalut and Sandakphu (3,600-3,800 m altitude)

Abies with *Rhododendron*

(f) Between Bakkim and Jongri (3,100-3,600 m altitude)

Tsuga with *Abies* and *Rhododendron*

(g) Gamothang (3,800 m altitude)

Rhododendron—*Abies*

(h) Selap and above (2,600-2,800 m altitude)

Quercus—*Tsuga*—*Rhododendron*—*Pieris*

(i) Above Walunchung Gola (3,500 m altitude)

Abies—*Rhododendron*—*Juniperus*—*Berberis*—*Betula*

(j) Thakma Khola (2,800-3,500 m altitude)

Tsuga, *Rhododendron*—*Arundinaria*—*Daphne*—*Abies*—*Tsuga*—*Rhododendron*—*Rosa*—*Thamnocalamus*—*Schefflera*—*Acer*.

(k) Bhuspate Danra (3000 m altitude)

Canopy : *Quercus*—*Tsuga*—*Rhododendron*—*Taxus*.

Undergrowth : *Berberis* species, *Viburnum* spp., *Magnolia*, *Ligustrum*, *Rosa*, *Daphniphyllum*, *Symplocos*, *Gaultheria*, *Pogostemon* etc.

Rhododendron forest is abundant at the top of Mt. Singalila and together with small patches of *Abies spectabilis* and deciduous trees, extends to Chia Bhanjang.

(5) ALPINE SCRUB AND MEADOWS :—The *Rhododendron* forest marks the timber line at an altitude of 4,000 m, the area up to 5,000 m. altitude is occupied by alpine meadow with prostrate *Juniperus squamata* and low bushes of *Rhododendron* species.

(6) TEMPERATE DECIDUOUS FOREST—This type does not occur in this region as a continuous vegetational zone, it is normally found in small patches on northern or eastern slope in the evergreen oak

and the *Rhododendron* forest zone. Species of *Acer*, *Betula*, *Magnolia*, *Prunus*, *Viburnum*, *Schefflera* are found in this zone.

(7) *DAPHNIPHYLLUM* FOREST—At the top of Bhandukay Bhanjang (3,100 m. altitude), a forest of *Daphniphyllum himalayense* including some species of *Rhododendron* has been found.

(b) GRASSLAND—A grassy community though not common in this region, is observed on the south faced steep rocky slope at Siling Tzokupa (3,800 m alt.). Its components are species of *Arundinella*, *Calamagrostis*, *Cymbopogon*, *Dunthonia*, *Helictotrichon* etc.

4.3 Succession of Vegetation at different elevations of a Hill Station (Darjeeling): In a botanical excursion to Darjeeling and its neighbourhood one gets the best source of information regarding the succession of vegetation at different altitudes or elevations.

Actual visit to Darjeeling reveals the nature of flora at different elevations, so Darjeeling is the best hill station for such study.

Darjeeling is situated at an altitude of about 2,011.5 m above the sea level. The neighbourhood of Darjeeling are Ghum (elevation about 2,269.5 m), Senchal (about 2,700 m.), Tiger hills (2,895.5 m) and Kurseong (about 1,402 m). So one should study the flora from Kurseong to Darjeeling, Ghum, Senchal starting from Sukhna in the plains.

The following characteristics are noted in the flora. The flora is divided according to elevation :

(1) The tropical or lower hill zone beginning from the plain up to 914.4 m.

(2) The sub-tropical or middle hill zone beginning from 914.4 m upwards up to 1,828.8 m or so.

(3) The temperate or upper hill zone beginning from 1,828.8 m up to 3,048 m.

(4) Above 3,657.6 m the flora is Alpine.

The following associations can be observed in the lower hill zone i.e., in the elevations beginning from plains i.e. Sukhna, Siliguri up to 914.4 m (just up to Tindharia or so).

1. *Shorea* (Dipterocarpaceae)—*Terminalia* (Combretaceae)—*Garuga* (Burseraceae) association, characteristic of lower hill or tropical zone.

2. *Schima* (Theaceae)—*Bauhinia* (Caesalpineae) association.

3. *Eugenia* (Myrtaceae)—*Phoebe* (Lauraceae) association.

In the sub-tropical or middle hill zone which ranges from 914.4 m—1,828 m or so, the following associations are come across :—

1. *Castanopsis* (Fagaceae) — *Schima* association.

2. *Schima* — *Castanopsis* — *Phoebe* association.

3. *Engelhardtia* (Juglandaceae) — *Castanopsis* — *Betula* association.

4. *Ostodes* (Euphorbiaceae) association.

In the middle hill or sub-tropical zone the majority of trees are evergreen. The common arboreal species is the *Castanopsis indica*.

Engelhardtia—*Castanopsis*—*Schima*—*Betula* association is the characteristic of greater parts of sub-tropical zone or middle hill zone. Here the rainfall is heavy. The association consists of high percentage of *Engelhardtia spicata* (at Kurseong on the road sides; *Castanopsis tribuloides*, *Schima wallichii* and *Betula cylindrostachys* are other common plants.

The *Ostodes* association ranges from 1,219—1,828·8 m.

In the temperate or upper hill zone where Darjeeling town and Ghum are located, the following associations are observed :—

1. *Machilus* (Lauraceae)—*Michelia* (Magnoliaceae) association.
2. *Quercus* association.
3. *Rhododendron* association.
4. *Tsuga*—*Abies* (Gymnosperms) association.

The temperate zone is characterised by great amount of humidity which favours the growth of mosses, lichens and other cryptogamic epiphytes on trees, so the trees present shaggy appearance. Thalloid bryophytes are represented by *Anthoceros* and *Marchantia*. The common moss is *Polytrichum*. All three classes of pteridophytes such as Filicales, Equisetales and Lycopodiales are found. The ferns are too numerous—the common and most striking is the tree fern (*Cyathea*), other common ferns are represented by various species of *Polypodium*, *Cheilanthes* (silver fern), *Onychium* (gold fern), *Botrychium*, *Equisetum*, *Lycopodium* etc. which are found at the elevation of 1,828·8 m or upwards. *Selaginella* is found everywhere in the sub-tropical as well as temperate zones of the eastern Himalayas.

The dicotyledonous arboreal vegetation in the temperate zone i.e. at Darjeeling proper consists mainly of the following plants :

Machilus spp., *Michelia cambellii*, *M. excelsa*, spp. of *Quercus*, *Betula*, *Bucklandia populnea*, *Rhododendron*, *Acer* etc. The gymnosperms also form the main bulk of tree forms, they are represented by *Cryptomeria japonica*, *Pinus longifolia*, species of *Juniperus*, *Thuja*, *Cupressus*, *Taxus* and *Podocarpus*.

The forest vegetation of Darjeeling is influenced by edaphic, biotic and climatic factors. At Darjeeling and places near about, the following species of plants are found.

Urticaceae—Species of *Lecanthes*, *Elatostema*, *Gerardiana heterophylla* var. *palmata* with stout stinging hairs and *Urtica parviflora*.

Betulaceae—*Betula alba*.

Polygonaceae—Numerous species of *Polygonum*, *Fagopyrum* and *Rumex*.

Fagaceae—Species of *Castanopsis* and several species of *Quercus*.

Berberidaceae—*Mahonia napaulensis* and species of *Berberis*.

Fumariaceae—*Dactylocapnos scandens*.

Guttiferae—Species of *Hypericum*.

Geraniaceae—*Geranium nepalensis*.

Oxalidaceae—*Oxalis* species.

Rutaceae—*Xanthoxylum ovalifolium* and *Boenninghausenia albiflora*.

Aquifoliaceae—*Ilex insignis*.

Saxifragaceae—*Hydrangea hortensis*, *Astilbe* spp. and *Dichroa febrifuga*.

Rosaceae—*Spiraea* spp., *Potentilla fulgens*, *Rubus* spp., *Pyrus* and *Prunus* spp.

Melastomaceae—Species of *Osbekia* and *Melastoma*.

Umbelliferae—*Hydrocotyle javanica* and *Oenanthe* spp.

Cornaceae—*Hewlingia himalaica* (found above 2,147 m)

Ericaceae—*Rhododendron* (several spp.), species of *Gaultheria*.

Plantaginaceae—*Plantago major*.

Gentianaceae—*Swertia* (several spp.), *Crawfordia* (2 spp.).

Labiatae—*Plectranthus coetus*, *Calamintha umbrosa*, *Notochaete* and *Salvia* spp.

Gesneriaceae—*Chirita urticifolia*.

Scrophulariaceae—*Calceolaria mexicana*.

Rubiaceae—*Luculia* (garden), *Rubia* (two spp.)

Valerianaceae—*Valeriana hardwicki*.

Dipsacaceae—*Dipsacus* (above 2,438 m)

Campanulaceae—*Campanula chlorata*.

Cucurbitaceae—*Sechium edule* (cultivated), *Edgaria darjeelingensis*, *Herpetospermum* spp.

Compositae—*Anaphalis* spp., *Eupatorium cannabinum*, *Artemisia* spp., *Aster* spp. (growing wild).

Orchidaceae (both terrestrial and epiphytic)—Numerous species of *Dendrobium*, *Microstylis wallichii*, *Coelogyne cristata*, *Phajus* spp. etc. : *Satyrium nepalense*, a very small common ground orchid with pink flowers.

4.4. Vegetation of Assam Valley : Assam valley comprises the tract of the Brahmaputra valley in the State of Assam which is bounded on the North by the Himalayas, on the East by the Mishini Hills, on the South by the patkoi range and the Naga, North Cachar, Jaintia, Khasi and Garo Hills and on the West by Sankosh river. Assam valley also includes the districts of Sibsagar, Lakhimpur, Darrang, Nowgong, Kamrup, Goalpara, parts of Balipara Frontier Tracts and Sadiya Subansiri and hill districts of Khasi, Jaintia and Garo Hills.

The climate of Assam valley varies from sub-tropical to tropical type. The rainfall is more variable and extremely well distributed throughout the year. In the lowest rainfall area the number of rainy days varies from 62—82 while the higher rainfall areas have 90—125 rainy days,

Three major formations have been recognised by Rowntree (1954) in the region and these are : (1) the tropical *Cinnamomum*—*Amoora*—*Michelia* formation, (2) the deciduous *Tetrameles*—*Stereospermum*—*Cedrela* formation and (3) the deciduous *Shorea*—*Dillenia*—*Lagerstroemia* formation.

1. THE TROPICAL CINNAMOMUM-AMOORA-MICHELIA FORMATION—This formation occurs throughout the wet zone with a mean annual rainfall of over 150 cm. This is considered to be the climax formation of the plain of the Brahmaputra valley and the surrounding foot hills up to a height of 1,000m. *Cinnamomum*—*Amoora*—*Michelia* formation is divided into two main associations e.g. (a) *Dipterocarpus*—*Mesua*—*Michelia* association that extends along the foot of the Patkoi range and Naga hills and between the Noa Dehing and Doyang rivers. It is found in the hills up to a height of 1,000 m and also extends in the plains. The mean annual rainfall over most of the area lies between 190 and 280 cm and is well distributed throughout the year. The main tree of this association is *Dipterocarpus macrocarpus* which forms about 40 per cent of the vegetation. *Dipterocarpus macrocarpus* is replaced by *Shorea assamica* at higher altitudes. Those two species occur either scattered or in patches, hence they never form dominants. *Vatica lanceaefolia* and *Mesua ferrea* are very common, they form real dominants and pure stands in places. Lianes and climbers are common and the trunks and branches of the trees are covered with epiphytes. Of climbers, *Vitis latifolia* is very interesting one which contains pure water—a good source of refreshment to the thirsty forester. Gymnosperm is represented only by *Podocarpus neriifolia*. The most common species of this association are : *Altingia excelsa*, *Amoora wallichii*, *Artocarpus* spp., *Canarium* spp., *Castanopsis* spp., *Cedrela toona*, *Chukrasia tabularis*, *Cinnamomum* spp., *Dipterocarpus macrocarpus*, *Michelia* spp., *Lagerstroemia* spp., *Shorea assamica*, *Eugenia* spp., *Schima wallichii* etc. as dominant tree layer ; *Bambusa pallida*, *Dendrocalamus* spp., *Litsaea* spp., *Magnolia* spp., *Vatica* spp. etc. as subordinate tree layer, *Ficus fistulosa*, *Alchornea latifolia*, *Alpinia* spp., *Calamus* spp., *Clerodendron* spp., *Ardisia depressa* etc. as shrub layer ; species of *Acanthus*, *Amomum*, *Begonia*, *Colocasia*, *Leea*, *Asplenium*, *Piper* etc. as field layer ; *Aeschynanthus acuminata*, *Bulbophyllum careyanum*, *Dischidia* spp., *Eria paniculata*, *Ficus villosa*, *F. rostrata*, *Hoya arnottiana*, *Pothos cathcarti*, *Raphidophora lancifolia*, *R. hookeri* etc. as epiphytes and *Acacia pennata*, *Dalbergia stipulacea*, *Delima starmentosa*, *Limacia cuspidata*, *Strychnos wallichiana*, *Thunbergia grandiflora*, *Vitis latifolia*, *Sabia limoniacea* etc. as climbers.

(b) The *Cinnamomum*—*Amoora* association. This association is found on the North bank from Subansiri to the Bornadi river as a

more or less continuous belt. On the South bank, the association is noted in the plains of Lakhimpur, Sibsagar and Nowgong districts as isolated patches and also in the Mikir hills. To the West, evergreen forests are confined to patches on slopes and in deep ravines. The optimum mean annual rainfall varies from 200 to 250 cm. The common species of this association are: *Alianthus grandis*, *Amoora wallichii*, *Mesua ferrea*, *Canarium bengalense*, *C. resiniferum*, *Dysoxylum hamiltonii*, *Michelia* spp., *Phoebe* spp., etc as dominant tree layer; *Bambusa pallida*, *Dendrocalamus hamiltonii*, *Achronychia laurifolia*, *Macaranga* spp., *Symplocos spicata*, *Meliosma simplicifolia*, *Pseudostachyum polymorphum*, *Talauma hodgsoni* etc. as subordinate tree layer; *Allophyllus cobbe*, *Calamus* spp., *Boehmeria* spp., *Clerodendron* spp., *Coffea bengalensis*, *Dracaena* spp., *Fragaria indica*, *Gnetum gnemon*, *Impatiens* sp., *Leea* sp., *Sambucus javanica*, *Livistonia jenkinsiana*, species of *Polypodium*, *Selaginella*, *Strobilanthes* etc. as shrub and field layer and species of *Ficus*, *Hoya*, *Dendrobium*, *Pothos*, *Dischidia* etc. as epiphytes.

Bor (1938) has described another association viz.. "the *Mesua*—other species Post-Climax" occurring in this formation. This association is found in the foot hills of Balipara Frontier Tract. The average height of the dominant species is 30m. The main species is *Mesua ferrea* which represents 80 per cent of the vegetation. Climbers are rare and species of *Ficus* are the common epiphytes.

Bischofia—*Dillenia* association is another association characteristic of the tropical *Cinnamomum*—*Amoora*—*Michelia* formation. This association occurs in low-lying areas subject to being flooded and submerged for some period. *Bischofia javanica* and *Dillenia indica* are the two main species of this association, besides *Lagerstroemia flos-reginae*, *Vatica lanceaefolia*, *Artocarpus chaplasha*, species of *Calamus* may be found.

2. THE TETRAMELES-STEREOSPERMUM-CEDRELA FORMATION—In this formation, only one association viz. *Cinnamomum*—*Amoora* association is recognised, which occurs on the ridges and slopes throughout the area. This association occurs roughly between Lumding to the West and Dimapur to the East and occupy the valley lying between the Mikir hills on the North and North Cachar and Naga hills to the South. The mean annual rainfall varies between 110 and 150 cm.

The main dominant species is *Phoebe goalparensis* which is considered to be a Post-climax Formation. Other principal species occurring in this association are *Tetrameles nudiflora*, *Stereospermum chelonoides*, *Amoora wallichii*, *Astonia scholaris* etc. which are all tall trees. *Dryptes elliptica*, *Alphonsea ventricosa*, *Amoora chittagonga*, *Bauhinia purpurea* etc. occur as middle sized trees. Among climbers *Acacia pruinescens*, *Combretum decandrum*, *Derris elliptica*, *Tapiria hirsuta*, *Vitis latifolia* are common. Shrubs and field layer are represented by *Clerodendron infortunatum*, *Coffea bengalensis*, *Ageratum conyzoides*, *Dzadalacanthus nervosus*, *Eupatorium odoratum* etc.

(3) **THE DECIDUOUS SHOREA-DILLENIA-LAGERSTROEMIA FORMATION**—This formation occurs in plains around Lanka and Hojai which are surrounded on the North and East by the Mikir hills and on the South-west by the North Cachar and Jaintia hills. This is the driest area in the Brahmaputra valley. Two associations have been recognised in this formation e.g., (a) the *Shorea*—*Lagerstroemia* and (b) the *Dillenia*—*Lagerstroemia*—*Albizzia* associations. *Shorea robusta* is the dominant species in the former and *Lagerstroemia parviflora* in the latter. Other species occurring in both the associations are *Bauhinia purpurea*, *Bombax malabaricum*, *Dillenia scabrella*, *Eugenia operculata*, *Erythrina stricta*, *Cassia fistula*, *Eupatorium odoratum*, *Imperata cylindrica*, *Saccharum spontaneum* etc.

4.5 Vegetation of Sunderbans: Refer article 5.7 (F) of Ecology portion.

4.6 Vegetation of the Gangetic Plain: The Gangetic Plain botanical province is a vast stretch of land in North India from West to the East comprising provinces of Uttar Pradesh, Bihar, West Bengal and part of Orissa. It is agriculturally the richest part of India. Geologically, the Gangetic Plain is of recent origin which formed in course of ages by silt of the Ganges and its tributaries. Botanically, it is not a single province but includes three provinces e.g., (a) flora of the *Upper Gangetic Plain* typified in North-western region, (b) flora of the *Middle Plain*—represented by the vegetation of Bihar, Orissa and West Bengal and (c) flora of the *Lower Plain* or *deltaic area* represented by the vegetation of Sunderbans. The vegetation of the Gangetic Plain presents three assemblages of ecological types e.g., mesophytic, hydrophytic and semi-xerophytic.

The Upper Gangetic Plain includes all the country drained by the Ganges and its North and South tributaries from North-west of Delhi to U.P. The indigenous vegetation in its western part is like that of dry country, during dry season trees are leafless for the most part; the grasses and other herbs dry up. The flora of the western extreme is indicated by species of *Peganum* (Zygophyllaceae), *Pluchea* (Compositae) and *Tecoma* (Bignoniaceae), these are continuous with the dry districts of the Indus Plain. The principal forest is that of Ajmere characterised by *Anogeisus pendula* (Combretaceae) and by species of *Boswellia* (Burseraceae), *Balsamodendron* (Burseraceae), *Moringa* (Moringaceae), *Rhus* (Anacardiaceae), *Acacia* (Mimosae) and *Prosopis* (Leguminosae). The common rose (Rosaceae) occurs in cold season along with other annual herbaceous plants. Families Leguminosae, Gramineae, Cyperaceae and Compositae occur in order of prevalence. Savannah of grasslands of considerable extent occur sometimes and are dotted with trees like *Bombax malabaricum* (Bombacaceae), *Randia uliginosa* (Rubiaceae), *Butea monosperma* (Leguminosae) and *Zizyphus* species of the family Rhamnaceae palms are represented by *Phoenix sylvestris*, species of *Calamus*, *Borassus flabellifer*, *Areca catechu* etc.; bamboos, unless planted are almost absent.

The Middle Gangetic Plain takes in all the country to the East of a north-southline through Benaras of U. P. It is the evergreen country of India in which cultivation has greatly affected the flora. A huge sea of waving rice fields occupies the greater part. The villages are buried in groves of mango, jack fruits, betel nut, figs and palms—amongst the herbaceous vegetation the aroids (both wild and cultivated) are conspicuous. The pond vegetation is characterised by some typical hydrophytes like *Nymphaea* (Nymphaeaceae), *Ceratophyllum* (Ceratophyllaceae), *Vallisneria*, *Hydrilla*, *Ottelia* (Hydrocharitaceae), *Limnanthemum cristatum* (Gentianaceae) etc. In the eastern portion where the waters of the Ganges and Brahmaputra tend to overflow, the jhils or side canals and old river beds are characterised by a luxuriance of marsh grasses and Cyperaceae, typified by tracts of *Saccharum spontaneum*, species of *Cyperus*, *Scirpus* and *Typha* (Typhaceae). Among the trees that are found, many are introduced such as *Bombax* (Bombacaceae), *Polyalthia* (Anonaceae), *Eriodendron* species (Bombacaceae) and also common plants like *Poinciana regia* (Leguminosae), *Lagerstroemia flos-reginae* (Lythraceae), *Pterospermum acerifolium* (Sterculiaceae), *Casuarina equisetifolia* (Casuarinaceae) and *Artocarpus integrifolia* (Anonaceae). In the drier districts, *Acacia arabica* (Leguminosae) is a characteristic feature.

The lower Gangetic Plain is characterised by the flora of Sunderbans. (For Sunderban flora refer article 5.7 (F), Ecology portion).

4.7 Vegetation of the Indus Plain : The Indus Plain province includes some humid parts of Punjab and Himachal Pradesh, Rajasthan, West of Aravalli range, Cutch and Gujrat. In this region the rainfall varies greatly e.g. about 1,000.0 cm in humid regions to 5.0 or 7.0 cm per annum in dry parts.

The main trees of Indus Plain are *Bombax malabaricum* (Bombacaceae), *Sterculia urens* (Sterculiaceae), *Moringa* species (Moringaceae), *Boswellia serrate*, *Odina wodier*, *Aegle marmelos* (Rutaceae), *Pistacia integerrima*, *Prosopis spicigera*, species of *Acacia*, *Dulbergia* and *Mimosa* of Leguminosae, *Dichrostachys cinerea*, *Anogeissus pendula* (Combretaceae), *Cordia* species, *Tamarix* species and *Salix* species (Salicaceae). Saline tracts over wide areas contain many grasses like *Salsola*, *Sporobolus* species, *Andropogon jwarancusa*, *A. nardus* etc., among trees *Acacia arabica*, *Tamarix articulata* and *Butea monosperma* are noteworthy. Along the rivers *Tamarix dioica* is the commonest type together with *Populus euphratica*.

The flora of Indus Plain is poor in comparison with the adjoining western Himalayas and is naturally adapted to the semi-desert conditions. Irrigation in this province has greatly affected the natural flora. Shrubby vegetation as is to be expected largely takes the place of trees and among the herbaceous types there is strong element of the annual type of vegetation that can withstand prolonged periods of drought. The most conspicuous shrub is the xerophytic *Euphorbia royleana* (Euphorbiaceae), besides species of *Capparis*, *Zizyphus*,

Grewia, *Balanites*, *Calotropis*, *Alhagi*, *Cassia*, *Dodonea* and *Calligonum* are well represented.

The deltaic vegetation of the Indus resembles that of the Sunderbans. The only palms of the Indus Plain are the widespread *Phoenix sylvestris* and the local gregarious *Nannorhops ritchieana*. The hardy bamboo, *Dendrocalamus strictus* is the only natural representative of its class in the area.

4.8 Vegetation of Malabar : Malabar province includes the major parts of Maharashtra, Mysore and Kerala. This region has heavy rainfall and humid climate which characterise its luxuriant vegetation.

Malabar is one of the botanically richest areas in India. Its shores are skirted with *Cocos nucifera* (Cocoanut palms) and the villages surrounded with groves of *Areca catechu* (Betel-nut palms) and *Corypha umbraculifera* (Talipot palms) ; *Vateria indica* (Dipterocarpaceae) is also abundantly planted in many parts. The majority of the flora is Malayan type and identical with that of Ceylon. Teak (*Tectona grandis*, Verbenaceae) is abundant but *Santalum album* (Santalaceae) occurs only in the East and dry flanks of the Ghats. *Cassia* (Leguminosae) and *Elettaria cardamomum* flourish wild in the jungles. The most distinctive characters of the Malabar flora are primarily the excessive content of the members of the families Guttiferae, Dipterocarpaceae, Palmae, Bambuseae of Gramineae and secondly Sterculiaceae, Anacardiaceae, Meliaceae, Myrtaceae, Mclastomaceae, Araceae, Zingiberaceae and Orchidaceae.

The ravines and shady slopes near the undulating summits are occupied by thickest of small trees and bushes. These mountain-like structures rise from the West to extensive grassy downs and table lands seamed with densely wooded gorges generally termed 'sholas'. Sholas are covered with evergreen forest, some of the most conspicuous trees of such forest are *Michelia nilagirica* (Magnoliaceae), *Ternstroemia japonica* (Ternstroemiaceae), *Gordonia obtusa* (Theaceae) and species of *Ilex*, *Meliosma*, *Microtropis*, *Euonymus*, *Photinia*, *Viburnum*, *Eugenia*, *Symplocos*, *Glochidion* and most of the plants belonging to the families Araliaceae and Lauraceae.

The most common shrub of Nilgiri is *Strobilanthes* (Acanthaceae). Next come species of *Eurya* (Theaceae), *Vernonia* (Compositae) and *Ligustrum* (Oleaceae). Of climbers, *Rosa leschenaultiana* (Rosaceae), *Jasminum brevifolium* (Oleaceae), *Gardneria ovata* (Loganiaceae), *Gymnema hirsutum* (Asclepiadaceae) and *Elaeagnus latifolia* (Elaeagnaceae). Among conspicuous herbs, the species of *Impatiens* (Balsaminaceae) is a notable feature ; at the lower altitude in the 'sholas', *Hydnocarpus alpina* (Flacourtiaceae) and species of *Rhododendron* (Ericaceae) and *Vaccinium* (Ericaceae) stand out. Peat bogs are found in depressions of the Nilgiri hills towards their summits. The peat is composed of grasses, sedges, mosses and rushes. In Nilgiris, *Acacia melanoxylon* (Leguminosae)—an exotic element, is widely cultivated.

4.9 Vegetation of Deccan : This province includes the whole peninsula South of the Ganges valley and East of the Malabar Ghats comprising the provinces of Andhra, Madras, parts of Mysore, Maharashtra, Madhya Pradesh and Orissa.

The plateau of the Deccan terminates in the East in a lower range of hills—the eastern Ghats (the flora of which is still Deccan type), but from here to the sea the land falls more or less abruptly into what may be called according to Calder (1937) the Coromondal Sub-province (Fig. 2.3, 5a) with a flora distinct from that of true Deccan.

Throughout the Deccan plateau deciduous forests are the conspicuous features, evergreen types are noted on the coasts and slopes. *Shorea robusta* (Dipterocarpaceae) occurs near the Godavari but *Tectona grandis* (Verbenaceae) occurs at intervals over the whole Deccan area. Floristically, northern Deccan is linked with the temperate to sub-tropical flora of eastern and western Himalayas e.g., species of *Thalictrum* (Ranunculaceae), *Berberis* (Berberidaceae) and epiphytic orchids like *Lasianthus laurifolius*, *Pygium acuminatum*, *Dysoxylum procerum*, *Cyclostemon assamicus* etc.

The Deccan forest mainly consists of species of Sterculiaceae, Meliaceae, Leguminosae, Combretaceae, Bignoniaceae and Urticaceae. *Chloroxylon* (the Stain-wood), *Chikrassia*, *Soyimida* (the Indian Red-wood), *Cedrela* (Toon) are all important plants but the best known is *Santalum album* (Sandal-wood) to be found in Mysore and adjoining districts.

The herbaceous vegetation is represented by the members of the families Acanthaceae, Commelinaceae, Gramineae and Labiatae. The chief bamboos are the common *Bambusa arundinacea* and *Dendrocalamus strictus* and of palms the common dates are *Phoenix sylvestris*, *P. acaulis* and *P. humilis*; *Borassus flabellifer* and few species of *Calamus* are also common.

The vegetation of Mysore like that of the Carnatic further South is somewhat scanty. The table land is often barren and the hills are covered with low shrubby vegetation. But towards the West, the vegetation is more or less similar to that of the western Ghats—the Malabar type and considerable forests are found. The steep slopes of the eastern Ghats which come normally under the influence of the north-east monsoon are also densely wooded, here species of *Dipterocarpus*, *Pterocarpus*, *Acacia*, *Butea*, *Lagerstroemia*, *Terminalia*, *Diospyros*, *Tectona* and *Santalum* are found as dominant. The black cotton soils, which prevail over large areas in Deccan, are characterised by an assemblage of many indigenous plants like *Capparis divaricata*, *Acacia arabica*, *Prosopis spicigera*, *Parkinsonia aculeata*, *Balanites roxburghii*, *Cadaba indica*, *Zizyphus nummularia*, *Cassia auriculata*, *Calotropis procera*, *Jatropha glandulifera*, *Hibiscus trionum*, *Momordica cymbalaria* and *Cressa cretica*. Mangroves occur in the estuaries. Thickest thorny evergreen and deciduous trees and shrubs are found here and there.

SELECTED QUESTIONS

1. Enumerate the main floristic regions of the world. How are the predominant environmental factors responsible for this type of distribution ?
Refer article 1.2 and para 2 of chapter 1
2. Give a general account of phytogeographical regions of India as proposed by different authors.
Refer chapter 2
3. Draw a map of India showing different phytogeographical regions and mention one dominant family of each.
Refer chapter 2, for 2nd part refer chapter 4
4. What do you mean by endemism ? Describe the theories regarding the origin of endemic plants. Name some endemic plants of India.
Or. Write an essay on endemism with special reference to endemism in India.
Refer chapter 3
5. Describe in brief the factors responsible for endemism.
Refer article 3.2
6. Give an account of the flora of the Indo-Gangetic Plain or the Gangetic Plain.
Refer article 4.6
7. Give a concise account of the flora of W. Bengal.
Refer article 4.6
8. Write short notes on :—
(a) Phytogeographical regions of Himalayas—Refer chapter 2
(b) Endemism—Refer para one, chapter 3
9. Give a general account of the vegetation of India and its distribution.
Refer chapter 4
10. Give an account of the desert vegetation of India.
Refer article 6.7A (Plant Ecology)
11. Give a concise account of the vegetation of Deccan.
Refer article 4.9
12. Characterise the main flora of eastern Himalaya and compare it with that of western Himalaya.
Refer articles 4.2 and 4.1
13. Give a brief account of the vegetation of the Indus Plain of India.
Refer article 4.7
14. Describe the succession of vegetation at different elevations which you may have observed during visit to any hill station.
Refer article 4.3

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ECONOMIC BOTANY

CHAPTER 1

Introduction

Economic botany forms the *applied* part of plant science *i.e.* *Botany* as it deals with the botany of various types of plants which are most essential to man's well-being. It has several branches *e.g.*, (1) *agriculture* dealing with the cultivation and production of field and plantation crops like cereals, millets, pulses, oilseeds, sugar and strach crops, fibre crops and other miscellaneous crops ; (2) *horticulture* dealing with the cultivation and production of garden plants yielding vegetables, fruits and flowers ; (3) *forestry* dealing with the study of forest products like timber, rubber, gums, resins etc ; (4) *pharmacognosy* dealing with the study of medicinal plants regarding their propagation and preparation of drugs from them ; (5) *plant pathology* dealing with the diagnosis, treatment and prevention of plant diseases and (6) *plant breeding* dealing with the improvement and the production of plants or varieties of economic value through introduction, hybridization and mutation.

The various types of plant products are very essential to mankind. From the very beginning of the human race, man is dependant on plants for the essentials of his existence. The three major necessities of human life *e. g.* *food, clothing and shelter* are supplied mainly by plants. Man's most important need is food which comes from plants. Although man is partly dependant on the flesh of herbivorous animals regarding protein food, but such animals are equally dependant on plants like man as they are not able to manufacture their own food from raw materials. The other two prime necessities of life *i.e.*, clothing and shelter are also derived to a great extent from plant fibres and from plant wood respectively. Wood obtained from plants is used as structural material, besides wood is used as fuel and also contributes in the manufacture of rayon, paper, various chemicals etc. Fuel, other than wood *e.g.*, coal, petroleum etc. is derived from fossil plants. Fibres, obtained from different plant parts are used in the manufacture of fabrics for clothing, netting and cordage. Drugs, used to cure disease, are mainly plant products. The various types of raw materials used for industrial purpose are obtained from plants—tanning material, cork, dyestuffs, oils, resins, gums, rubber etc. are a few examples of such raw materials. So these are the examples of some plant products from which we can get an idea in which plants and plant products affect the welfare of mankind.

Besides the above mentioned value of plants as sources of food, clothing, drugs and raw materials for industry, plants also play important role in other ways *e.g.*, the effects of forests and other types of natural vegetation in controlling rainfall, erosion etc.

Plants never manufacture materials like fibres, wood, gums, resins, starch, sugar, alkaloids etc. for use to man. Most of the plant products are the results of plant metabolism, some of which are used directly in the welfare of the plant life while others represent waste products.

The most important function in the life of plant is *photosynthesis*, in this process manufacture of food directly from raw materials takes place. Grape sugar ($C_6H_{12}O_6$) formed in photosynthesis is utilised in various ways and which constitutes the plant's metabolism. The utilization of such grape sugar takes place in different forms involving several processes viz., (a) *the formation of cell walls that constitute the plant skeleton*—cell wall is composed of *cellulose*, a non-living material formed by plants from grape sugar ; (b) *the manufacture of new protoplasm*—a little part of the sugar is used directly either in the formation of new protoplasm or to replace the disintegrated protoplasm ; (c) *the elaboration of various types of food materials e.g., the carbohydrates* (sugar, starch, cellulose, hemi-cellulose, pectins, gums, mucilages etc.), proteins and fats either for storage as reserve foods or immediate use by plants ; (d) *the production of different types of secretions and excretions e.g., essential oils, pigments, tannins, resins, latex, waxes, alkaloids, glucosides, enzymes, organic acids, hormones etc.* and finally (e) the release of stored energy through catabolic process i.e., respiration. The former four processes involved in metabolism form the constructive i.e. *anabolic* phase of metabolism. In this phase, various substances that are useful to man and also to the plant are formed.

The number of plant species utilized by man for any purpose is estimated between 10,000 and 20,000 ; and those that are economically involved in human work and existence comes from about 1,000-2,000 species. The world's food crops are obtained from fifteen species, viz. rice, wheat, maize, barley, sorghum, sugarcane, sugarbeet, potato, sweet potato, cassava, bean, soyabean, groundnut, coconut and banana.

Classification of Economically Important Plants : According to Hill (1952) economically important plants may be classified as follows :—

I. FOOD PLANTS i.e. plants yielding various types of food. These include :

(a) *Cereals* i.e., plants yielding rice, wheat, maize etc.

(b) *Millets* i.e., plants yielding small-grained food stuff e.g. jowar, bajra, ragi, kaon etc.

(c) *Pulses* i.e., plants yielding various types of pulses like gram (chana), pea (matar), pigeon pea (arhar), lentil (musur), mung etc.

(d) *Vegetables* i.e., plants yielding vegetables like radish, carrots, sweet potatoes, potatoes, brinjals, cabbage and its allies, fruit vegetables, legume vegetables like beans of various types etc.

(e) *Fruits* i.e. plants yielding fruits like orange, banana, apple, guava, mango etc.

II. **FOOD ADJUNCTS** i.e., plants yielding spices, flavouring materials, beverages etc.

(a) *Spices and other flavouring materials* i.e., plants yielding spices like zinger, turmeric, cinamomum, cloves, saffron, pepper etc.

(b) *Beverages* i.e., plants yielding beverages like tea, coffee, cocoa, etc.

III. **DRUG PLANTS** i.e., plants yielding drugs.

(a) *Medicinal plants* i.e., plants yielding medicine e.g., cinchona, ipecac, rauwolfia etc.

(b) *Fumitories and Masticatories* i.e., plants yielding narcotics e.g., tobacco, opium, ganja etc.

IV. **INDUSTRIAL PLANTS AND PLANT PRODUCTS** i.e., plants yielding fibres, timber, rubber, tannin, gums, essential oils, sugars, cellulose products etc.

(a) *Fibre plants*—yielding fibres of various types e.g., cotton, jute, hemp, flax etc.

(b) *Timber plants*—yielding timber e.g., teak, sal, mahogany etc.

(c) *Rubber plants*—yielding rubber, e.g., *Hevea*, *Ficus elastica* etc.

(d) *Gums and Resin* yielding plants e.g. Pine, *Acacia* etc.

(e) *Essential oil* yielding plants e.g., mustard, castor, linseed, coconut, groundnut etc.

(f) *Tanning and dye* yielding plants e.g., Hemlock (*Tsuga canadensis*), indigo, *Bixa orellana* etc.

(g) *Sugar and starch* yielding plants e.g., sugarcane, sugarbeet etc.

Recently, Brouk (1975) has divided plants of economic importance into following seven classes :

(a) *Plants Consumed by Man*—cereals and pseudo-cereals, vegetables, fruits, nuts, plants providing extracts, flavourings, beverage plants, fumitories and masticatories, fermentative micro-organisms.

(b) *Shelter Plants.*

(c) *Ornamental Plants.*

(d) *Industrial Plants.*

(e) *Animal Fodder Plants.*

(f) *Medicinal Plants.*

(g) *Semantic Plants* : “are those that acquire economic importance as a result of some special significance.” Certain flowers have been accepted as national symbols in some countries. Magical properties and superstitious beliefs have also been associated with certain plants. Flowers are used to express our good feelings towards the person to whom these are presented !

Cereals and Millets

A. CEREALS

The cereals are the most important sources of plant food for mankind and also for lower animals since the earliest time. Certain plants of the family Gramineae whose grains are used as food are called cereals. The name 'cereal' has been given in honour of the Roman goddess 'Ceres', whom Romans once worshipped as the giver of grain.

Cereals are cultivated for their grains which form the foremost staple food of India and other Asian countries. Wheat, rice, maize etc. are the most important of all cereals; others are barley, oats and rye.

Regarding food value, cereals contain a high percentage of carbohydrates (68-79%), a considerable amount of proteins (7-16%) and some fats; vitamins are also present.

All cereals belong to the family Gramineae, which is characterised by caryopsis fruits, flowers grouped in spikelets, $\frac{1}{2}$ alternate leaves with ligules and open sheathing leaf bases, delicate and rounded stems and annual or perennial herbs mainly.

The world production of cereals (excluding Sorghum and Millets) in 1970 amounted to 1097.1 million tonnes.

In India the total annual area under cultivation of cereals is 205 million acres and the corresponding average production of grains is 56.5 million tonnes. In 1969-70 the production of cereals in India went up to 87.8 million metric tonnes.

2.1 Rice (*Dhan*, *Chawal*) : Rice is the staple food of the people in the eastern, southern and south-western parts of India. It is grown, practically in all states in India. The total area under cultivation in 1973-74 was 38 million hectares and the total production came to 43.7 million tonnes.

Rice can grow in varied physiological conditions, both in tropical and temperate regions, from sea-level to about 2,133.5 m above sea-level and from the semi-arid tracts of Rajasthan to the very wet areas of Assam, West Bengal, Mysore, Kerala and Maharashtra.

Oryza sativa L. is the botanical name of rice plant. It belongs to the family Gramineae. Plants are annual or sometimes perennial herbs. Leaves flat, linear, acuminate with 2-partite lanceolate ligule. Inflorescence spikelets arranged in panicle, drooping, rachis angular and channelled. Spikelets 3-flowered, lower two florets are represented by two empty lemmas; fertile lemma laterally compressed, finely granulate, hispid, ciliate, coriaceous, usually 3-5 nerved, awned

or not, as long as spikelet ; palea as long as lemma, keeled. Flowers bisexual, lodicules 2, bi-lobed, semi-fleshy ; stamens 6, filaments capillary. Style short, stigmas feathery and laterally exerted. Fruit caryopsis, oblong, angular, free or adnate to the lemma and palea.

Soil—Rice grows well on clayey loams to clays which, when puddled, turn into soft mud and on drying form cracks. It can also be grown on damp alluvial soils, sandy and stony soils, deep soils, terraced hill slopes etc.

Climate—Under high temperature and humidity, rice thrives best. But sufficient supply of water is necessary as the plant is semi-aquatic.

Cropping season—In tropical and sub-tropical regions the crop can be grown throughout the year. But in temperate regions like hills, the crop is grown only in the summer time of the year. The cropping seasons and the average yield per acre of three main types of rice in India are as follows :—

<i>Types of Crop</i>	<i>Sowing time</i>	<i>Harvesting</i>	<i>Average yield/acre</i>
1. Autumn— <i>aus</i> , <i>beali</i> or <i>kar</i>	May—June	September -- October	450—950 kg.
2. Winter— <i>aman</i> , <i>hain</i> or <i>karthika</i>	June --July	November -- December	1,500—1,900 kg.
3. Spring or Summer — <i>boro</i> or <i>jalua</i>	November -- December	March-- April	± 350 kg.

In W. Bengal, Assam, Bihar, U.P., Punjab, M.P. and Maharashtra June-July is the optimum time for sowing medium and long duration varieties. In South India *double cropping* (i.e. production of the crops on the same land in one year) is commonly practised—in this case a quick maturing variety is followed by a long duration type or *vice versa*. In recent years with the introduction of short duration, non-photosensitive varieties, the system of double or even triple cropping is now being used in most of the rice growing states of India depending on availability of water for irrigation.

Rotation—In deltaic areas, in heavy rainfall areas and in lowlands having stagnant water, rice is grown year after year with a fallow in between. But where lands are provided with irrigation facilities, there the crop is rotated with wheat, sugarcane, plantain, betelvine, sometimes pulses, sannhemp, irrigated garden crops etc.

Cultivation—Firstly, preparation of land for sowing is necessary, this preparation depends upon whether the crop is to be grown under the 'dry' or the 'puddle' system. In former case, the land is ploughed immediately after the harvest of the previous crop and then brought to tilth by repeated ploughing or harrowing when rains are available. Weeds and stubbles of the previous season are collected and burnt on

the field. Manures if applied, are added well in advance before sowing. In case of puddle system, the land is first irrigated about a month before sowing and then ploughed in standing water. The ploughing is repeated for three or four times to stir up and puddle the soil thoroughly. Finally, the puddled soil is levelled by the help of ladder over the field or by other manual labour. The levelling of paddy field is essential to hold irrigation water evenly. The field is then made into several plots, the size of which ranges from 1/10th acre to 1/40th acre ; each plot is provided with watertight *bunds*.

Sowing—Under 'dry' system of cultivation, seed¹ is sown in heavy rainfall areas in rows ; in moderately heavy rainfall areas, sowing is done by broadcasting. Line sowing is done with the help of three or four coulters drills or by hand. In case of 'puddle' system of cultivation, seed is sown by broadcasting after sprouting it slightly or unsprouted. For broadcast sowing, seed rate varies from 34 kg.-54 kg. per acre and for line sowing from 27-34 kg. per acre.

For transplanted crops, seedlings are raised in either 'dry' or 'wet' nurseries. The soil, in both the cases, is prepared in the same technique as for the 'dry' and 'puddle' system of growing the main crop. The seed beds are about 1.2m wide raised beds having a suitable length, they are separated from each other by 0.3m wide channels for irrigation. In W. Bengal, generally 2-3 seedlings of 3-5 weeks age are transplanted at each hole. Normally, early varieties are planted 15.2 cm from line to line and 15.2 cm from plant to plant while medium and late varieties are planted with 22.8 cm × 15.2 cm or 22.8 cm × 22.8 cm spacings.

Manuring—Nitrogen, either in organic or inorganic form, is the best manure for rice. Application of 13.5-18 kg. of nitrogen i.e. 67.9—99.5 kg. of ammonium sulphate per acre gives better yield. Other types like farmyard manure, compost, oil-cakes, fish manure, green twigs, leaves of Leguminous plants like *Indigofera*, *Tephrosia* etc. and green manuring with *dhaincha* are also in common use in different parts of the country. 9-18 kg. of P_2O_5 i.e. 56.5-113 kg. of superphosphates per acre is also applied during puddling. For high yielding varieties the requirement of fertilizers, for obtaining satisfactory yield, is higher i.e. 80-100 kg. N, 50-60 kg. P_2O_5 and 50-60 kg. K_2O per hectare, of course depending on fertility status of the soil.

After-Care—In the field, water is allowed to stand to a depth of 1.2-2.5 cm until the transplanted seedlings are well established. After this, about 5.0 cm of water with frequent draining and re-irrigating is maintained in the field up to the dough stage of the crop. For quick and uniform maturation of grain, water is drained off from the field a week or two before harvesting. Few weedings either by hand or with a 'rotary weeder' should be given up to the

¹ Only pure viable seed of improved varieties or dressed seed with fungicides.

boot leaf stage of the crop, at the same time the soil near the roots of the plants should be stirred.

Harvesting, Threshing and Storage—The crop is harvested when the 'ears' are nearly ripe and the colour of the straw is still slightly green. Crop is cut with sickles by farmers, dried in the field for few days (3-4), stacked in the threshing yard for a week and then threshed either with sticks, or by beating against a wooden log or treading the entire crop under the feet of bullocks. Finally the husk is removed by pounding method or by rice hullers.

Generally cleaned unhusked paddy is dried and stored in jute bags and granaries of different types.

Yield—Depending on the variety grown, soil condition and manuring, irrigation, season and method of cultivation, the yield of paddy varies from 453 kg.—2,265 kg. per acre. Under similar conditions, the yield of *aus* paddy varies from 450 kg.—950 kg. per acre; the yield of *aman* paddy varies from 1,500 kg.—1,900 kg. per acre while *boro* paddy yields about 350 kg. per acre in India. The yield figures hold good for traditional, indigenous varieties only.

Uses : The grain is used as food. The rice straw is used for making straw boards, mats and papers. Rice bran oil is used for making soaps and cosmetics.

Varieties—Generally rice varieties are classified as *early*, *medium* or *mid-late* and *late* maturing. In some states they are also called *autumn*, *winter* and *spring* or *aus*, *aman* and *boro* types respectively. About 628 improved strains have been developed in India of which 202 varieties are reported to be under cultivation. Some of the important rice varieties recommended for West Bengal are :—

Aus :—(a) Dular (hybrid), (b) Dhairal, (c) Charnock, (d) Ashkata, (e) NC 1626, (f) NC 918 etc.

Aman :—(a) Badkalamkati—65, (b) Churnakati, (c) Rupsail, (d) Indrasail, (e) Nagra 41/14, (f) Bhasamanik, (g) Patnai-23, (h) Latisail, (i) Raghusail, (j) NC 678, (k) NC 1281, (l) Tilakkachair, (m) Kumragore, (n) SR 26B, (o) FR 43B, (p) Basmati, (q) Badshabhog, (r) Randhunipagal, (s) Sitabhog etc. [The last 4 varieties are fine and scented.]

Boro : (a) Chinsura Boro-1, (b) Latisail

High yielding varieties of rice :

Recently some varieties have been released in India—either through introduction or by hybridisation which are capable of high yield, show response to application of Nitrogenous fertilizers, short statured and non-lodging, generally non-sensitive to photoperiod, possessing little or no dormancy and thus capable of fitting into double or triple cropping systems. Some of the popular high yielding rice varieties are : (i) *early* : Cauvery, Bala, Pusa 2-21, IR-28, IR-30 etc. ; (ii) *medium-early* : Kanchi, Padma, Ratna, Krishna, IR-22, IR-26, IR-29 ; (iii) *Medium* : IR-8, Jaya, IR-20, Jayanti, Sonu ; (iv) *Late* : Vijaya, Pankaj, Jagannath, Mashuri etc. The yield potential of these varieties goes even up to 8,000 kg/ha. or more.

Diseases and Insect Pests—The important rice diseases are :—(a) Blast caused by *Pyricularia oryzae* ; (b) Bunt caused by *Neovossia horrida* ; (c) Helminthosporium blight caused by *Cochliobolus miyabeanus* ; (d) Foot rot or Bakanae disease caused by *Gibberella fujikuroi* ; (e) Irregular stem rot caused by *Helminthosporium sigmoideum* var. *irregularae* ; (f) Leaf smut caused by *Entyloma oryzae* ; (g) Bacterial leaf blight caused by *Xanthomonas oryzae* ; (a), (b), (c) and (d) can be controlled by treating seeds with Ceresan or Agrosan GN before sowing, spraying with 1% Bordeaux mixture and growing resistant varieties. For (e) and (f), control measures are not yet known.

Important rice insect pests are :—

(a) Paddy stem borer (*Schoenobius incertellus*) can be controlled by destroying stubbles after harvest, dipping seedlings in 0.1% DDT suspension before transplanting and spraying the crop with 0.025% Parathion or 0.08% Endrin in the field @ 270-360 litres per acre.

(b) Paddy cutworm (*Cirphis unipunctata*) can be controlled by dusting 5% BHC @ 6.5-9.0 kg. per acre.

(c) Paddy bug (*Leptocoris varicornis*)—can be controlled by shaking plants so that young nymphs may drop in water, by dusting plants with 5% BHC @ 5.5-6.7 kg. per acre.

(d) Rice grasshopper (*Hieroglyphus banian*)—can be controlled by dusting with 6-10% BHC @ 9.0 kg. per acre and spraying with 0.02% Aldrin at 270-360 litres per acre.

(e) Rice hispa (*Hispa armigera*)—can be controlled by dusting with 5% BHC at 6.7 kg. per acre and spraying with 0.25% DDT @ 270-360 litres per acre.

2.2 Wheat (*Gam Gehon*) : Next to rice, wheat is the most important staple food for Indian people. This crop plant is widely cultivated in U. P., Punjab, Madhya Pradesh, Maharashtra, Bihar and Rajasthan. In India, the crop is at present grown on an area of about 19 million hectares producing about 11.5 million metric tonnes of grains. Production of wheat in 1972 was 26.4 million metric tonnes.

Triticum aestivum L is the botanical name of the bread wheat plant which is cultivated extensively in major parts of India. Other species are :—*Triticum durum* (Macaroni wheat)—cultivated on the black soils of Central and Peninsular India ; *Triticum dicoccum* (Emmer wheat) is grown in Mysore, Andhra Pradesh, Nilgiri hills of South India and Maharashtra ; *T. sphaerococcum* (Indian dwarf wheat) is cultivated in Punjab along with *T. aestivum*.

Triticum aestivum (wheat) belongs to the family Gramineae. Plant is annual herb. Leaf blades linear, flat, auricled. Inflorescence—erect spikes ; spikelets solitary, sessile, laterally compressed, 2-several flowered. Glumes ovate, sub-equal, persistent, often unequal sided, obtuse or shortly awned. Lemmas oblong, ventricose, muticous or 1-3 awned ; palea equalling the lemma, 2-keeled. Lodicules 2, entire, ciliate. Stamens 3. Styles very short. Grain oblong, ventrally grooved.

Climate—Indo-Gangetic plain is the best wheat producing region as the winter of this region is cool and the crop can grow for a period of 6 months. Areas having moist and warm climate are not suitable for this crop. Continuous drought, specially in unirrigated tracts, hampers the production of wheat. The growth period of the crop is temperature limited—high temperature of either end of the season reduces it. Within a rainfall range from 130-1,000 mm, wheat is grown effectively.

Soil—The best soil for the cultivation of wheat is easily irrigable and drainable loamy or clay-loamy soils. In Indo-Gangetic Plain, wheat is grown well in the irrigated alluvial land, whereas the black soil tracts of Maharashtra, Madhya Pradesh and South India are equally important for wheat cultivation.

Rotation—This practice is done in different ways in various parts of India. In the irrigated alluvial tracts of Punjab, U.P. and Rajasthan, the commonest rotation is wheat following a *kharif* crop like jowar, bajra or cotton in previous year. For green manuring, leguminous crops like pulses can be grown in the immediately preceding *kharif*. Linseed, gram, peas, *brassicas* etc. are also rotated in many places. In low-lying areas (W. Bengal), an early paddy is taken before wheat. In the black soil tracts of Central and South India, unirrigated wheat is rotated with *kharif* jowar or cotton in the preceding year. The growing of wheat mixed with pulses (gram, peas, arhar, lentils), linseed, barley, safflower etc. is pretty common throughout India.

Cultivation—For uniform and healthy germination, the seed bed should be well-pulverised and compact. Several ploughings, repeated harrowing in the rainy season followed by 3 or 4 cultivations and planking immediately before sowing produce a good seed bed for unirrigated crop on alluvial soils. For irrigated crop, the land is irrigated before sowing and the number of ploughings is reduced. Seed, only highly viable and free from weed seeds and seed borne diseases, is sown by broadcasting, drilling or dibbling at the rate of 90 kg. per hectare normally. Sowing is started in the middle of November. Line sowing (15-22 cm apart) with drills at about 5 cm depth deposits the seed in moist soil which results in good germination and plant stand. In hills, regular dibbling (25 cm \times 12 cm) is generally practised. In rough, dry and light soils, deeper sowing is the general rule while in moist or heavy lands, comparatively shallower sowing is desirable. Transplanting is done at 25 cm \times 25 cm spacing and it has to be fertilised with 35 kg. nitrogen per hectare.

For irrigated wheat crop, first watering should be given one month after sowing. Irrigations (2-4) at tillering, heading and grain-filling stages are essential. Weeding is also equally important which may be done by spraying 2, 4-D (1.3-2.5 kg. per hectare acid equivalent in water) though hand weeding is generally practiced.

The dry (non-irrigated) wheat crop is not normally manured although application of well-rotted farmyard manure or compost or oil-cake at the rate of 180-275 quintal per hectare about six weeks before sowing has been suggested. For irrigated wheat, application of 35-45 kg. per hectare of nitrogen together with 25-35 kg. per hectare of phosphoric acid and farmyard manure (in case of phosphate deficient soils) is recommended. In some areas for better yield, green manuring together with the addition of superphosphate is practised. For high yielding varieties of wheat, the optimum dose of fertilizers is, 100-120 kg. N, 50-60 kg. P_2O_5 and 40 kg. K_2O per hectare ; however the actual dose should be determined on the basis of soil test data.

Harvesting—Harvest begins in mid January to April depending on variety when the grain is deadripe and the straw is golden yellow and brittle. Plants are uprooted either by hand or cut by sickle.

Harvested grains are then threshed normally by treading under the feet of cattle on a threshing floor. Next winnowing is done with winnowing baskets.

Storage—Thoroughly dried grains should be stored in moisture-proof and fumigated store rooms.

Yield—The yield of unirrigated or rainfed crop varies from 450 kg. per hectare (in Mysore) to about 675-775 kg. per hectare in M.P., U.P., Punjab and W. Bengal. The yield of irrigated crop ranges from 1,000 kg. per hectare (in South India) to 1,400 kg. per hectare in the Indo-Gangetic Plain. It has been observed that, under, favourable conditions of cultivation and manuring, the irrigated crops yield more than 1.2 metric tonnes of grain per acre. The recently released dwarf high yielding varieties, however, are capable of yielding over 5-6 metric tonnes per hectare.

Uses : The whole-meal flour is used in making ordinary and loaf-bread, biscuits and other confectionary. The wheat straw i.e. chaff is fed to cattle and also used in the manufacture of paper.

Varieties—About 90 recommended varieties of wheat for different States are there. Of these varieties recommended for W. Bengal are N. P. 710, N. P. 798, N. P. 824 and N. P. 835 for plains and for hills N. P. 781, N. P. 809 and Ridley.

The recently released high yielding varieties of wheat in India are—(a) Sonora 64, (b) Lerma Rojo, (c) Chhoti Lerma, (d) Safed Lerma, (e) Kalyan Sona, (f) Sonalika, (g) Sharbati Sonora, (g) Janak, (i) Girija etc.

On the basis of grain characters, some varieties of wheat are normally sold in the regional markets under the following trade names :—

- (1) Sharbati (*T. aestivum*)—Grains are hard, amber coloured, small to medium sized.
- (2) Dara (*T. aestivum*)—Colour of the grain is a mixture of white and red.
- (3) Dudhia or Pissi or Dudhya (*T. aestivum*)—Soft and white grains.
- (4) Lal Kanak (*T. aestivum*)—Hard or semi-hard red grains.
- (5) Desi, Lal, Lal pissi, Waji or Bajia (*T. aestivum*)—Soft red grains.
- (6) Bansi or Bakshi, Jalalia, Malwai, Piwla or Pilva Kathia, Katta, Bijapur or Kemp godi (*T. durum*)—White, amber or red grains.
- (7) Khapli or Jod (*T. durum* ?)—Hard, long, slender and reddish grain.

Diseases and Insect Pests :

Common wheat diseases :—(a) Bunt caused by *Tilletia foetida* and *T. caries*—it can be controlled by treating seeds with Cerasan or Agrosan GN @ 2 gms. per kg. and growing resistant varieties.

(b) Flag smut caused by *Urocystis tritici*—can be controlled by growing resistant varieties and following crop rotation.

(c) Karnal bunt caused by *Neovossia indica*—can be controlled by growing resistant varieties.

(d) Leaf rust (Brown rust) caused by *Puccinia recondita* (= *P. triticina*)—control like that of (c).

(e) Stem rust (Black rust) caused by *Puccinia graminis tritici*—can be controlled by growing resistant varieties, by dusting with sulphur @ 6.7-9.0 kg. per acre or spraying with zinc sulphate or parate @ 2.25 litres + 336 grams per 450 litres water per acre.

(f) Strip rust (Yellow rust) caused by *Puccinia striiformis* (= *P. glumarum*)—can be controlled by growing resistant varieties.

(g) Loose smut caused by *Ustilago nuda* (= *U. tritici*)—can be controlled by growing resistant varieties.

(h) Bacterial ear rot or Tundu caused by *Corynebacterium tritici*—can be controlled by using clean seeds free from galls for sowing.

Common wheat insect pests :—

(a) Stem borer (*Sesamia inferens*)—can be controlled by spraying 0.03% Endrin @ 270-360 litres per acre.

(b) Wheat aphid (*Schizaphis graminum*)—can be controlled by dusting with 3-5% BHC at 6.7-9.0 kg. per acre or spraying with 0.05% nicotine at 270-360 litres per acre.

(c) Termites (*Microtermes obesi*)—can be controlled by adding a chemical mixture of 5% BHC, Aldrin or Chlordane dust in the soil @ 9.0-11.3 kg. per acre before sowing.

(d) Surface grasshopper (*Chrotogonus* spp.)—can be controlled by dustin with 5% BHC @ 6.7-9.0 kg. per acre.

2.3 Maize (*Bhutta*, *Makka*): Maize forms mainly the staple food of the people of northern India though it is cultivated to some extent all over the country. In India, maize was introduced from America at the beginning of 17th century.

Maize grain is very nutritious, it contains easily digested carbohydrates, proteins and very few deleterious substances.

In India, the average annual area under maize is about 4.4 million hectares; the annual output of the grain is about 3.9 million metric tonnes. Production in 1969-70 is 5.67 million metric tonnes.

Zea mays L. is the botanical name of the maize plant. It belongs to the tribe *Maydeae* of the family *Gramineae*. Plant is tall, annual, large herb, monoecious. Stem solid. Leaf blades flat, long and broad, distichous, sheaths overlapping. Male inflorescence terminal in spiki-form dense flowered panicle raceme. Female inflorescence axillary, covered by series of spathes, the rachis is thick and spongy. Male spikelet paired—one sessile, the other shortly pediceled. Basal glumes of male spikelets membranous, many nerved; male florets 2 in each spikelet—lower and upper lemmas membranous, hyaline, 3-5 nerved; palea with incurved margins. Lodicules thick cuneate, stamens 3; pistillode often present. Female spikelet 2-flowered, the lower floret is very rudimentary or absent. Lower and upper basal glumes fleshy at base, membranous at top, shortly ciliated, broad rounded. Lower lemma hyaline, membranous; upper lemma short, subtending female flower, shortly pointed; upper palea concave. Lodicules absent in female flower; styles short, connate; stigmas very long—much exerted as tuft of hairs. Grain globose or obovate flat in series, crowded on spongy cob.

Climate—Maize can grow in tropical as well as temperate zones up to an altitude of 1,800 m or more. Actually maize is a *warm season* crop, hence it can be grown throughout the year in areas of mild climate. The average annual rainfall required for the cultivation

of maize is 75 cm. Artificial irrigation is only required when it is cultivated in dry summer season.

Soil—Maize grows best on well drained, fertile loamy soils which are neither too heavy nor too light.

Rotation—Maize is generally grown in rotation with wheat, barley, sugarcane or cotton in the following year ; in hilly tracts, potatoes often follow maize. Normally maize is grown pure, but sometimes pulses or beans are grown as subsidiary crop along with it.

Cultivation—A fine seed-bed is necessary for the cultivation. Immediately after the harvesting of *rabi* crops, the soil should be given several ploughings (4-6) with the light plough : each ploughing must be followed by planking. Care should be taken to make the soil well pulverized, fairly compact and free from weeds.

Heavy manuring is essential for maize ; 25-38 cartloads of cattle manure or compost per hectare is the normal rate. Nitrogen is applied to the soil at the rate of 55 kg. per hectare as the optimum dose. For hybrid maize, 100-125 kg. nitrogen per hectare is applied in equal doses at three stages e.g. at sowing, knee-high and tasseling stages. At sowing time, soil may be manured with phosphorus and potassium at the rate of 50-75 kg. per hectare.

In northern India, seeds of rainfed grain crop and irrigated fodder crop are sown usually by broadcasting method at the rate of 15 - 20 kg. per hectare (for grain crop) or 40-45 kg. per hectare (for fodder crop) ; but irrigated grain crop is sown in rows behind the plough or is dibbled. In other parts of India, both the irrigated and rainfed (unirrigated) crops are sown in rows, either in furrows behind the plough or with the help of a drill. The rainfed (unirrigated) grain crop is sown in June-July or in May as in the hills or in April-May as in some other parts ; in the canal tracts of Punjab it is sown in August. The irrigated crop for green cobs or for fodder is sown in March-April. The rows are spaced 60-75 cm apart (for grain crops) or 30 cm apart (for fodder crop) and the plants in each row spaced 30-35 cm apart.

Artificial irrigation is required if the rain is not adequate and well distributed, otherwise not. The crop needs careful weeding at young stage, one or two hand weeding followed by 2-3 hoeings are sufficient for better growth of the plant.

Harvesting—After the cobs become fully mature i.e. when the sheaths turn brownish and the seeds become more or less hard and dry, then harvesting is done. Cobs are spread in the sun to dry, and then beaten with sticks to separate the grain. Use of maize shellers are gradually coming in vogue.

Yield—The average yield of irrigated crop is about 1,700-1,800 kg. per hectare which may be increased (after heavy manuring) up to 3,800 kg. per hectare. Depending on the fertility of the soil, the yield of unirrigated crop varies from 675-1,350 kg. per hectare. The

yield of hybrid and composite varieties varies between 4·5 and 8 metric tonnes per hectare.

Uses—Maize is used in various ways. It is also grown as fodder for livestock : the immature cobs are eaten after roasting ; the grains are used in making corn starch and industrial alcohol as well.

Varieties—On the basis of the texture i.e. hardness and softness and sugar content of the grain, maize can be classified into following varieties :—(a) *flint*, (b) *dent*, (c) *sweet*, (d) *pop*, (e) *waxy*, (f) *soft* or *floury* and (g) *pod*.

In India, *flint* variety is cultivated chiefly : *dent* variety is generally cultivated in hilly tracts.

Hybrid maize—Now-a-days, local varieties are becoming obsolete and gradually going to be replaced by the double cross hybrids produced and released under the All India Co-ordinated Maize Breeding Programme. Important among the hybrid maize varieties are : (i) Ganga 101, (ii) Ranjit, (iii) Deccan, (iv) Ganga Safed 2, (v) Hi-Starch, (vi) Ganga 3, (vii) Ganga 5, (viii) Himalayan 123. Besides, in recent years some high yielding *Composite* varieties of maize have also been released, viz : (a) Jawahar, (b) Ambar, (c) Vijay, (d) Sona, (e) Vikram, (f) Kissan etc. The yield of the composite varieties is as high as the hybrid ones, but the advantage is that the farmers can use their own seeds provided, these are produced in isolation from other maize crop. They are also fairly resistant to diseases and tolerant to drought.

Diseases and Insect Pests :

Important diseases of Maize—(a) Downy mildew caused by *Sclerospora philippinensis*—it can be controlled by spraying with Bordeaux mixture or other fungicides like Fytolan, Perconox etc., by growing resistant varieties etc.

(b) Head smut caused by *Sphacelotheca reiliana*—can be controlled through crop rotation and sanitation.

(c) Leaf blight caused by *Helminthosporium turcicum*—control like that of (b) and by growing resistant varieties.

(d) Smut caused by *Ustilago maydis*—control is like that of (c).

(e) Brown spot caused by *Physoderma zeamaydis*—control is like that of (b).

Important insect pests of Maize—

(a) Maize stem borer (*Chilo zonellus*)—can be controlled by destroying stubbles after harvest and also spraying the crop (when one month old) with 0·32% DDT @ 162-360 litres per acre.

(b) Leaf roller (*Marasmia trapezalis*)—can be controlled by destroying rolled leaves and larvae, also by spraying with 0·25% DDT @ 270-350 litres per acre.

(c) Maize grasshopper (*Hieroglyphus nigrorepletus*)—can be controlled by destroying eggs through ploughing after harvest and dusting adults with 5–10% BHC @ 6·7–9·0 kg per acre.

B. MILLETS

Millet is a kind of cereal with *minute* seeds, belonging to the family Gramineae. The important millet crops which are grown largely in different parts of India are :—

(1) Common millet (*Panicum miliaceum*), (2) Finger millet (*Eleusine coracana*), (3) Italian millet (*Setaria italica*), (4) Barnyard millet (*Echinochloa colonum*), (5) Bulrush millet (*Pennisetum typhoides*), (6) Kodo millet (*Paspalum scrobiculatum*), (7) Little millet (*Panicum miliare*), (8) Sorghum (*Sorghum vulgare*) etc.

Millets are used for forage and as a food for both man and domestic animals. Millets are most oldest of known food grains and in China these have been growing since 2700 BC. Eastern Asia is the probable home of the origin of millets. In India, millets are cultivated in more than 40,000,000 acres of land.

2.4 Bulrush millet or Pearl millet (*Bajra*): Bajra or Pearl millet is one of the most important millet crops. It furnishes an important food for poor people. Grains are edible, the flour made from the grains is very nutritious and is used for bread or cake. Plant stalks i.e. straws are used as a fodder and also for thatching purpose.

In India, this millet is cultivated in the Punjab, U. P., Rajasthan, Maharashtra, Madras and Andhra Pradesh. Production of Bajra during 1969-70, was 5.33 million metric tonnes.

Bajra is obtained from *Pennisetum typhoides* (Burm. f.) Stapf. & Hubb. (Syn. *P. typhoideum* L.). Plant is annual tall herb reaching up to a height of 4.5 m. Stem often stout. Leaves small, flat or broad-rolled in bud condition. Inflorescence spikiiform panicle, 3-8 in number, compact and cylindrical. Spikelets ovate, small, solitary or in clusters of 2-3 or 5, surrounded by simple or branched feathery bristles. Florets 2, lower male or neuter, upper bisexual; lower basal glumes minute or absent; lower lemma paleate or epaleate; upper lemma coriaceous, upper palea ciliate, 2-nerved. Lodicules small or absent. Stamens 3, anthers bearded. Grains dorsally compressed.

Climate—Bajra grows well in warm climate having a low rainfall ranging from 381.00-508.00 mm per annum. Light showers followed by bright sunshine favour the growth of this plant.

Soil—Bajra requires poorer types of soil such as sandy, shallow mixed black and gravelly soils for better growth.

Rotation—Bajra may be grown either as a pure crop or as mixed crop. As a pure crop, it is rotated with jowar, ragi, cotton etc. As a mixed crop, it grows along with gram, mung, tur, sesamum, castor etc.

Cultivation—After the first shower the land is ploughed or harrowed 2-3 times. Before sowing, the soil may be manured with farm-yard manure. The sowing time varies according to the nature of the crop—the dry crop is sown in the middle of July, the rainfed crop is sown in May with the commencement of early rain while the irrigated crop is sown in March or April. Seeds are sown either by broadcasting or in rows 30-38 cm apart by drills at the rate of 2.5-5.5 kg. per acre (for pure crop) or 1.6-3.5 kg. per acre (for mixed crop). For hybrid bajra the fertilizer dose is 80-100 kg. N, 30-40 kg. P_2O_5 and 40 kg. K_2O per hectare; the application of phosphate and potash recommended if the soil is found deficient on the basis of soil test.

Next, few operations like one hand weeding and one or two hoeings are given to the crop.

Harvesting and Threshing—The crop matures in October or November. Plants are cut close to ground and stacked in the field to dry—then only mature earheads are removed and carried to threshing floors where grains are threshed out by treading under the feet of cattle. Winnowing is done with the help of baskets.

Yield—The average yield of the crop in different states of India varies between 135.9 and 407.7 kg. of grain per acre.

Varieties : Though there were several varieties of bajra in cultivation, these were not good yielders and rather restricted in adaptation. In recent years several hybrid bajra varieties have been produced and released for cultivation. These are (i) HB 1, (ii) HB-2, (iii) HB-3 and (iv) HB-4 : they yield up to 4.5 tonnes per hectare under irrigated condition and 2.3 tonnes/ha. under unirrigated condition.

Diseases and Insect Pests—Most common diseases of Pearl millet are—(a) Green-ear disease caused by *Sclerospora graminicola* and (b) Rust caused by *Puccinia penniseti*—these can be controlled by growing resistant varieties. Important insect pests are (a) Deccan wingless grasshopper (*Colemania sphenareoides*) and (b) Leaf roller (*Murasmia trapezalis*)—former can be controlled by dusting with 5%—10% BHC @ 6.7—9.0 kg. per acre and latter by spraying with 0.25% DDT @ 270—330 litres per acre.

2.5 Finger millet (Ragi, Marwa) : It is one of the major food crops of the agricultural people in South India and Maharashtra. The grain is nutritious. Ragi flour is used for cake, porridge and pudding. A kind of beer-like fermented beverage is made from the grains by the local people.

In India, ragi is grown on large scale in Madras, Andhra Pradesh, Mysore, Maharashtra and to some extent in Bihar, U.P. and Orissa. The annual average cultivated area and production are about 3.7 million acres and 1.7 million tonnes respectively. Production in 1969-70 is 2.11 millions metric tonnes.

Finger millet i.e. ragi is obtained from *Eleusine coracana* Gaertn. (Family Gramineae). Plant is annual, tall grass. Stem tufted. Leaves broad. Spikelets in digitate or umbellate and stout spikes, laterally compressed 3-12 flowered; florets bisexual, 2—3 seriate and secund; rachilla continuous between the lemmas. Basal glumes slightly unequal, persistent; upper obtuse, acute, keeled. Lemmas usually 3-nerved. Palea smaller than lemma. Lodicules 2, cuneate. Grain globose, free.

Climate—Medium climate, having rainfall between 508.0 and 1016.0 mm is suitable for ragi cultivation. During hot season, it can be grown as an irrigated crop.

Soil—Ragi grows well on red, light red, light black, ashy and sandy loams or even on well drained alluvial loams.

Rotation—Rainfed ragi is rotated with jowar, gram, sesame, niger etc. while irrigated crop is rotated with garden crops like potatoes,

brinjal, sweet potato, chillis, sugarcane etc. Ragi may also be grown alone or mixed with bajra, jowar etc.

Cultivation—After the commencement of the rainy season, the land is prepared by two or three ploughings or harrowings. The crop is manured with farmyard manure or compost at the rate of ten cartload per acre; besides, for irrigated crop, a mixture of ammonium sulphate and super phosphate at the rate of 22.5 kg. per acre may be applied. Seeds are sown either by broadcasting at the rate of 4.5-13.5 kg. per acre or in lines 25 cm apart by drills or in furrows behind the desi plough. Ragi is also transplanted with 4-5 weeks old seedlings. This is done in falling rain, generally 2-3 seedlings are placed in each point. Next weeding and thinning operations are done by the help of hand and bullock hoe.

Harvesting and Threshing—After the maturity of the crop within 3-5 months, the plants are cut close to the ground; then tied into sheaves and stacked to dry. Sheaves are threshed either by beating with sticks or treading under the feet of bullocks.

Yield—The average yield of dry crop varies from 226.5-307.7 kg. of grain per acre.

Diseases and Insect Pests—Common diseases are :—(a) Blast caused by *Pyricularia oryzae*—control measure is same as under rice (b) Charcoal rot caused by *Macrophomina phaseoli*—can be controlled through proper sanitation. (c) Downy mildew caused by *Sclerophthora macrospora*—can be controlled by crop rotation and (d) Helminthosporium leaf blight caused by *Helminthosporium nodulosum*—can be controlled by treating seeds with Agrosan GN @ 2 gms. per kg. before sowing. *Insect pests* are same as under Bajra.

2.6 Italian or Fox-tail millet (Kaon, Kakum) : It is cultivated in many parts of the country including plains and hilly tracts but the main centre of cultivation lies in Andhra Pradesh and Tamil Nadu. The native home of this millet was probably eastern Asia.

Italian millet is used as food and fodder. It is also used medicinally as diuretic and astringent and also for rheumatism. When used for food, the grains are boiled or parched.

Italian or fox-tail millet is obtained from *Setaria italica* Beauv. (Fam. Gramineae). Plant is annual herb with narrow or elliptic-ovate flat leaves with bristly apex. Inflorescence dense spike with innumerable bristles. Spikelets oblong ovate, dorsally much convex, falling entire from the pedicels subtended by persistent bristles; florets 2, lower male or sterile, upper bisexual. Basal glumes very dissimilar, lower much smaller 3-5 or 1-7 nerved; upper basal glumes 5-7 nerved; lower lemma empty or male paleate, dorsally furrowed or wrinkled. Upper lemma enclosing upper palea by margins, smooth, usually rough or pitted, hardened in fruit. Stamens 3. Styles free.

Climate—Plants are drought resistant, for better growth they require scanty rain and moderate to high temperature.

Soil—It can grow on various soils like alluvial loams, red loams, clayey soils, black cotton soils etc.

Rotation—Italian millet is grown either pure or mixed with cotton, ragi etc.

Cultivation—The crop is raised both under rainfed and irrigated conditions. The land is ploughed once thoroughly and then harrowed twice or thrice. For irrigated crop, manuring with farmyard manure at the rate of 5-6 cartloads per acre is necessary. The rainfed crop is sown in May or June-July while irrigated crop is sown in January-February or March-April according to climatic condition. The seed is normally sown by broadcasting at the rate of 2.6-4.5 kg. per acre; in case of mixed crop sowing is done in separate rows by the help of drill. Next one weeding is done for pure crop. For mixed crop, interculturing along with subsidiary crop is necessary. In case of irrigated crop, watering at the intervals of 7 to 10 days is done till the crop matures.

Harvesting and Threshing—The ripe earheads are cut, heaped on threshing floor for a week to dry and then threshed under the feet of cattle or with the help of a stone roller.

Yield—The yield of rainfed pure crop varies from 180-350 kg. of grain per acre.

Diseases and Insect Pests—Important diseases of Italian millet are :—(a) Blast caused by *Piricularia oryzae*—control measure is same as under rice : (b) Rust caused by *Uromyces setariae italicae*—can be controlled by growing resistant varieties ; (c) Smut caused by *Ustilago crameri*—can be controlled by treating seeds with Agrosan GN @ 2 gms. per kg. before sowing and (d) Downy mildew caused by *Sclerospora graminicola*—can be controlled by growing resistant varieties.

Common insect pests—same as under Bajra.

CHAPTER 3

Pulses and Legumes

Next to cereals, pulses and legumes are the most important sources of human food. Pulses contain high amount of proteins, more than any other vegetables, hence they are nearer to animal protein in food value. Pulses are highly nutritious, easily grown and mature rapidly. They have high energy content. In addition to protein, carbohydrates and fats are also present in pulses, pulses are also rich in minerals and vitamin B. Majority of pulses possess root nodules that contain nitrogen fixing bacteria—these bacteria can fix free nitrogen from the air and thus increase the soil fertility.

All pulses belong to the sub-family Papilionaceae of the family Leguminosae which is characterised by having *legume* or *pod* type of fruit (developing from monocarpellary gynoecium and dehiscing along two sutures), *one* carpel, *marginal* placentation, racemose type of inflorescence and mostly compound leaves with *pulvinus* leaf base.

In India, the total annual area under the cultivation of pulse crops is about 57 million acres and the corresponding average production of pulses is about 10.9 million tonnes. Production of pulses in 1969-70 was 11.6 million metric tonnes.

3.1 Gram or Chick pea (*Chola, Chana*) : It is the oldest known pulse crop grown in India. Gram or chick pea is a native of southern Europe, now successfully grown in U.P., Bihar, Punjab, Rajasthan and Madhya Pradesh.

The seeds of the plant are edible, cotyledons of seeds are used in the form of '*dal*', '*besan*' etc., the vegetative parts are used as salad and fodder. For the treatment of scurvy disease, germinated seed is very useful. Green leaves contain malic and oxalic acids and are prescribed for intestinal disorders.

In India, average annual area for cultivation and production is about 23.7 million acres and 5.7 million tonnes of crop respectively. Total production of gram in India during 1969-70 was 5.54 million metric tonnes.

Cicer arietinum is considered to have originated in Western Asia and spread at a very early date to India and Europe. Gram (whole seed) contains 61.2 per cent carbohydrates, 5.3 per cent fat and 17.1 per cent protein, among other constituents.

Cicer arietinum L. is the botanical name of chick pea or gram. Plant is small bushy annual herb. Leaves even-pinnate compound, rigid, stipulate; leaflets and foliaceous stipules strongly veined and deeply toothed, the rachis ending in a tendril or bristle or with a

leaflet. Flowers axillary solitary, bracts small. Sepals 5, connate in an oblique tube. Petals exerted; standard broad and narrowed to a wide claw; wings obliquely obovate, free; keel incurved. Stamens 10, diadelphous, anthers uniform. Ovary sessile, one chambered, 2-many ovuled; style filiform, incurved, beardless; stigma terminal, capitate. Fruit an oblong sessile turgid pod, narrowed into the persistent style. Seeds sub-globose or irregularly obovoid; hilum small, funicle slender.

Climate—Gram grows best in areas where rainfall ranges from low to moderate and weather is mild cold. Generally gram is grown as a dry crop in *rabi* season.

Soil—Gram can be grown in light alluvial soil (in Upper India) or in black cotton soils and water-retentive clay loams (in South India and Bombay-Deccan respectively).

Rotation—Gram can be grown alone or mixed with linseed, barley, wheat and mustard. It is also rotated with wheat, bajra, jowar, rice or jute.

Cultivation—Several ploughings and repeated harrowings are given to the soil but no fine tilth is attempted and the soil is left loose. The soil is rarely manured, but phosphate and nitrogen at the rate of 8-11 kg and 2 kg per acre respectively is conducive to good yield. Seeds are sown by broadcasting or in rows about 30 cm apart in the middle of October and November. The seed rate varies from 10-36 kg per acre in different states of India. The crop is rarely weeded. Few irrigations are given in case of acute drought. In case of luxuriant plant growth, shoots are topped off to encourage branching and flower formation.

Harvesting and Threshing—The crop matures in 150 days, sometimes in 90-120 days in Bombay-Deccan and South India. The plants are harvested when leaves become dry reddish brown and start shedding. Harvested plants are dried for about a week and then threshed by beating with sticks or trampling under the feet of bullocks.

Yield—The average yield of grain of unirrigated crop varies from 226 to 272 kg per acre. Under irrigated conditions, yield varies from 679 to 806 kg per acre.

Diseases and Insect Pests—Common diseases of gram are :—(a) Blight caused by *Mycosphaerella rabiei*; (b) Root rot caused by *Opercullella padwickii*; (c) Rust caused by *Uromyces cicerisartictini*; (d) Stem rot caused by *Sclerotinia sclerotiorum*; (e) Wilt caused by *Fusarium orthoceras* var. *ciceri*—all these may be controlled by growing resistant varieties.

Common insect pests are :—(a) Gram caterpillar (*Heliothis obsoleta*)—can be controlled by dusting with 5% BHC or DDT @ 6.7-9.0 per acre or spraying with 0.16% DDT suspension @ 370 litres per acre. (b) Red gram plume moth (*Exelastis atomosa*)—control measures same as for (a). (c) Gram pod fly (*Agromyza obtusa*)—can be controlled by sowing resistant varieties or spraying with 0.05% nicotine sulphate or 0.25% DDT @ 246-370 litres per acre. (d) Greasy cutworm (*Agrotis ypsilon*)—can be controlled by mixing 5% DDT in soil before sowing, dusting with 5% DDT or Aldrin at the base of plants @ 6.7-9.0 kg. per acre or spraying the base of plants with 0.031% Aldrin @ 246-370 litres per acre. (e) Peas semilooper (*Plusia orichalcea*)—control measures same as for (a).

3.2 Mung or Green gram (*Sona mung, Moong*): Green gram or Mung is obtained from *Phaseolus aureus* Roxb. (Syn. *P. mungo* Auct. non Linn., *P. radiatus* Auct. non Linn.). This plant is grown as a pulse crop all over the country, but most important producing states are Madhya Pradesh, U. P., Punjab, Bihar, Rajasthan and West Bengal. The grains or seeds are used as pulse or 'dal', green pods as vegetables and haulm and husk as fodder for cattle. In West Bengal, seeds are known as the *golden mung* or '*sona mung*'.

Green gram is one of the very ancient legumes of India. Seeds are small and oval, they are highly nutritious containing proteins (23.6%) and phosphorous. Unlike other pulses, it is easily digestible without producing any flatulence or heaviness.

The botanical name of green gram or mung is *Phaseolus aureus* Roxb. Plant is a sub-erect herb. Leaves pale green, pinnately 3-foliate, stipules membranous, lanceolate, small or conspicuous. Flowers fasciculate and copiously racemose, peduncles axillary with rachis nodose. Sepals 5, connate in a campanulate tube. Petals exerted, standard orbicular, sub-auriculate at base, wings ovate or oblong; keel prolonged in a beak to form a spiral. Stamens 10, diadelphous. Ovary sub-sessile, many-ovuled, style enclosed in beak of keel; stigma oblique. Pod distinctly reflexed, coriaceous, not septate between the seeds. Seeds thick, smooth, yellow.

Climate—The plant grows best in areas where rainfall is well distributed and ranges from 63.5 to 88 cm per annum. Heavy rains, even damp winds at the time of flowering and fertilization may cause great harm.

Soil—It thrives well on deep, well-drained loamy soils of North as well as on red and black soils of Peninsular and Southern India.

Season and Rotation—Green gram is normally grown as a rainfed *kharif* crop. In some parts of India it is cultivated in the *rabi* season as a second crop after paddy. In hilly tracts, up to 1,329 m, green gram is grown as a summer crop. The *kharif* crop may be grown either alone or mixed with and subsidiary to maize, bajra and some millets whereas the *rabi* crop is grown unmixed.

Cultivation—For the pure crop in the *kharif* season, two or three ploughings and then harrowing are given to the land to get a rough tilth. For mixed crop, separate tillage is not necessary as it gets tillage given to the main crop in the mixture. Manuring is done with superphosphate and ammonium sulphate at the rate of 45-67.5 kg. and 11 kg. per acre respectively. The *kharif* crop is sown in June-July whereas *rabi* crop in September-October. Seeds are sown either by broadcasting or by drilling in furrows behind a plough or in rows 22.5-30 cm apart. Seed rate per acre varies from 4.5 to 11.5 kg. (when sown alone) and from 0.9 to 2.7 kg. (when sown as a mixed crop). Weeding and sometimes hoeing operations are given to young plants. Flowering takes place in about 60 days and the crop matures after another 3-4 weeks.

Harvesting and Threshing—Before the ripening of the crop, unripe pods are picked for use as green vegetables. Normally the crop ripens in 90 days, though some early varieties ripen in 60 days. The crop is harvested before it is dead ripe. Harvested crop is dried on threshing floor for 7 or 10 days, then threshed by treading under bullocks or by beating with sticks.

Yield—For a pure crop, the average yield of grain varies from 226.5 to 271.5 kg. per acre whereas that of a mixed crop varies from 67.9 to 135.9 kg. per acre.

Diseases and Insect Pests—Common diseases are :—(a) Anthracnose caused by *Glomerella lindemuthianum*—can be controlled by using healthy seeds, following crop rotation practice and growing resistant varieties; (b) Bacterial bean blight caused by *Xanthomonas phaseoli-indicus*—control measures same as for (a); (c) Bean rot caused by *Phytophthora parasitica*—can be controlled by spraying 1% Bordeaux mixture; (d) Bean blight caused by *Ascochyta phaseolorum*—can be controlled by destroying infected plant debris and spraying with 1% Bordeaux mixture; (e) Leaf spot caused by *Cercospora* spp.—control measure is same as for (c); (f) Powdery mildew caused by *Erysiphe polygoni*—can be controlled by growing resistant varieties and dusting the crop with fine sulphur powder and (g) Rust caused by *Uromyces appendiculatus*—can be controlled by growing resistant varieties.

Common insect pests are :—(a) Agromyzid flies—control measures same as for gram pod fly. (b) Lycaenid butterflies—can be controlled by spraying 0.16% DDT @ 370 litre per acre or by handpicking caterpillars.

3.3 Black gram (*Mashkalai*, *Urd*): Black gram is obtained from *Phaseolus mungo* Roxb. It is cultivated as pulse crop in Madhya Pradesh, U. P., Punjab, Maharashtra, West Bengal, Andhra Pradesh and Mysore.

Black gram is very rich in protein and phosphoric acid. It is used as 'dal', in preparing 'papar' and 'bori'. In W. Bengal, dal obtained from *Phaseolus mungo* is called 'Beauli' or 'Kalai dal.'

Phaseolus mungo Roxb. differs from *Phaseolus aureus* in following characters :—

Stem diffuse; pods erect or sub-erect, seeds grey or black.

Climate—Both in warm plains and cool hills up to an altitude of 1,829 m, it is grown as rainfed crop. Moist climate is best for better growth and yield of black gram.

Soil—The crop grows best in water-retentive stiff loamy or heavy soils. It also thrives well on black cotton soil and brown alluviums.

Rotation—Normally, black gram is grown as a mixed crop, subsidiary to cotton, maize, jowar etc.

Cultivation—Preparation of land, tillage, manuring, method of sowing are similar to those described for green gram. Depending on the climatic and agricultural conditions and the variety grown, seeds are sown either in February or June-July or October-November, and the seed rate is 10 to 15 kg. per acre.

Yield—Average yield of grain varies from 226.5 to 316.5 kg. per acre.

Diseases and Insect Pests—Same as under Mung.

3.4 Soyabean (*Geri kalai, Bhat, Ramkurthi*) : It is obtained from *Glycine hispida* (Syn. *Glycine max* (L.) Merr., *G. soja, Soja max*) belonging to the sub-family Papilionaceae of the family Leguminosae. It is a native of South-East Asia and its first cultivation was recorded in China in 2838 B. C. In India, soyabean is now cultivated in the Punjab, Himachal Pradesh, Kashmir, West Bengal, the Khasia and Naga hills, hilly tracts of Assam up to an altitude of 1,822 m, Manipur and Bihar.

In some countries of East Asia, soyabean is grown mainly as a food crop. Soyabean, with about 40% high quality protein is the richest source of vegetable protein. Soyabean protein contains all the essential amino acids in large quantities. In addition to proteins, soyabean contains considerable amount of vitamins and minerals, specially calcium in rich quantity. The seeds of soyabean are used as pulse. Green seeds are used as vegetables; roasted and salted seeds are used in cakes and candies. The oil obtained from the seeds is edible and semi-drying in nature, and is used in cooking and also in the manufacture of soap, paints, varnishes and candles, printing ink, linoleum, insecticides, disinfectants etc.; oil-cake is used as fodder. The flour, obtained from the seeds, contains low carbohydrate and high protein which is an excellent food for diabetics. Seeds are processed to give milk-like products, curd or cheese. Soyabean milk extracted from the seed, is used as substitute of *caesin* in the preparation of sweets also. Now-a-days soyabean has become a highly essential and vital crop. At present artificial "meat", made from soyabeans, has been developed by a Japanese food manufacturer—this "meat" will be used for mixing into processed meat such as saussages, meat balls and meat paste¹.

Glycine hispida is an annual sub-erect or twining herb covered with hairs, reaching up to a height of 1.8 m. Stem erect or climbing. Leaves trifoliate, ovate-lanceolate, long petioled. Flowers small, white or purple to reddish purple on short axillary racemes. Sepals 5, connate in a campanulate tube, lobes equally distinct. Petals little exserted, standard sub-orbicular; wings narrow, keels obtuse. Stamens 10, monadelphous or at length diadelphous. Ovary sessile, style short, incurved, beardless; stigma terminal, capitate.

Pods 3.5-5 cm long in clusters of 3-5, densely hairy. Seeds elliptical, compressed, yellow or chocolate or black in colour.

Climate—Soyabean plant is practically a sub-tropical plant though its cultivation has been extended to temperate and tropical regions. Soyabean does not tolerate severe winter or much heat. Moist climate and shady conditions are favourable for the growth of soyabean. It is more susceptible to frost than other peas. Primarily, soyabean is a short day plant and is sensitive to the length of day.

Soil—Soyabean grows well in rich sandy or clayey loams or well drained alluvial soils. It can also grow in acid as well as in alkaline soil.

¹ A. B. Patrika dated 28th Dec. 1967—news from A. F. P.

Rotation—Soyabean is generally raised as *kharif* crop. It is grown either pure or in mixture with maize, in some parts with *aus* paddy also. Soyabean can be rotated with potato or sugarcane.

Cultivation—The land is thoroughly ploughed, cleaned and brought to a state of good tilth. Leaf mould or farmyard manures at the rate of 10—15 cartloads per acre may be applied on soils of low fertility. Seeds are sown at the outbreak of the monsoon (in June-July) in rows 5.0—7.6 cm. apart by broadcasting, the depth of sowing varies from 3.6—5.0 cm., the seed rate ranges from 6.5—9 kg. per acre when the crop is grown for seed, but when grown for fodder or green manure seed rate varies from 13.5—18 kg. per acre.

Harvesting—Early variety of soyabean ripens in 75-110 days while late variety takes 100—200 days. The crop is harvested when the pods are just ripe and leaves begin to fall off. Harvested crops are dried in the sun and then threshed on the floor by beating with sticks. Soyabeans, when raised for forage, are harvested at the half mature stage of pods; at this stage plants contain high percentage of digestible nutrients and are palatable.

Yield—The average yield of seeds varies from 294 kg. to 403 kg. per acre; under favourable conditions the yield sometimes reaches up to 1165.5 kg. per acre.

Varieties—Disoy, Verde, Kim, Kanrich, Bansai, Clark-63, BB-24-9-3, Bragg etc.

Diseases and Insect Pests—Important diseases are :—(a) Bacterial disease caused by *Xanthomonas phaseoli*—can be controlled by growing resistant varieties. (b) Downy mildew caused by *Peronospora* spp.—can be controlled by treating seeds with Agrosan GN before sowing and growing resistant varieties; (c) Dry root rot caused by *Macrophomina phaseoli*—can be controlled through crop rotation practice and growing resistant varieties and (d) Mosaic virus.

Insect pests—Same as under Mung.

3.5 Pea (*Matar*, *Muttar*): Pea is probably a native of southern Europe and S. W. Asia extending eastwards to the Himalayas including northern India. The earliest record of the cultivation of pea has been noted since before the beginning of Christian era.

There are two main groups of peas e.g., (a) field pea or 'desi matar', obtained from the plant *Pisum sativum* L. var. *arvense* Poir. (Syn. *P. arvense* L.) and (b) garden pea or 'gol matar' obtained from *P. sativum* L.

Pea plants are annual, glaucous, tendril bearing, climbing or trailing herbs. Leaves even pinnate, leaflets 1 to 3 pairs, rachis ending in a simple or branched tendril; stipule foliaceous. Flowers are coloured or white, axillary peduncled, solitary or in few-flowered racemes. Sepals connate in oblique tube, lobes 5. Petals much exserted, standard very broad, narrowed to a short, wide claw; wings oblong falcate, adnate in their middle to the short, incurved obtuse keel. Stamens 10, diadelphous. Ovary sub-sessile, many ovuled; style inflexed, bearded along the inner face, 3-cornered, dilated upwards throughout. Pods pendulous, turgid, continuous within, several seeded. Seed sub-globose.

Field pea has coloured flowers and angular coloured seeds. In

India, this pea is grown as a field crop in the Punjab, U. P., Himachal Pradesh, M. P., Bihar and Orissa for seeds which are used for human consumption in the form of pea meal or 'dal'. Other parts of plants are used for forage, silage and green manuring.

Garden pea has white flowers and round smooth or wrinkled seeds. It is usually grown in various parts of India e.g., Bihar, M. P., W. Bengal, Orissa as a garden vegetable. The seeds are eaten green or used for canning and its fleshy pods together with seeds are eaten sometimes by local people.

Both the varieties are very important as they are not only grown for pod and seed production but also for green manure, fodder and silage. They also increase the soil fertility by fixing atmospheric nitrogen with the help of nitrogen-fixing bacteria present in the nodules of their roots. Both the fruits and seeds are very rich in protein, vitamins and minerals.

Climate—Peas are mainly a cold season crop, they can withstand light frost.

Soil—Peas grow well on well-drained heavy types of soils e.g., loams and clay loams. They are sensitive to high soil acidity.

Rotation—Peas are either grown mixed with *rabi* crops like wheat and barley or grown alone in rotation with different cereals and other crops.

Cultivation—The land is ploughed and harrowed several times to make a mellow bed. Then it is more or less levelled and laid out into beds or ridges and furrows. For high yields, an adequate supply of fertilizers is necessary; a fertilizer dressing containing 4.5-9.0 kg. N, 22.5-31.5 kg. P_2O_5 and 23.5-31.5 kg. K_2O per acre is recommended. In the hills, the main crop of peas is sown from April to May whereas in plains from September to November; in some regions, a rainy season crop is sown in June-July. Peas are sown near the edge of raised beds, the width of which varies from 0.9 m—1.8 m. Seeds are sown either by broadcasting at the rate of 27-36 kg. per acre or with a drill in rows 30-65.8 cm apart at the rate of 11-27 kg. per acre. Spacing within the row varies from 5 to 7.6 cm. After sowing, seeds are covered with soil by planking or harrowing. During dry season, the crop is irrigated every 10-14 days.

Harvesting—Field peas are harvested after 5-6 months of their sowing when seeds are mature; at the time of harvesting, plants are cut near to ground. Harvested plants are then removed to threshing floor for drying, then they are threshed by treading under bullocks.

Garden peas are harvested for table use when pods are well filled.

Yield—Average yield of peas per acre is 2-2.5 metric tonnes.

Diseases and Insect Pests—Common diseases are: Fusarium foot rot and blight caused by *Ascochyta pinodella*, *A. pis*; bacterial blight caused by *Xanthomonas vignicola*; Downy mildew caused by *Peronospora pisi*; Powdery mildew caused by *Erysiphe polygoni*; Rust caused by *Uromyces fabae* and Seedling disease caused by *Pythium* spp.—all these can be controlled by proper sanitation, using resistant varieties, crop rotation practice and dusting with sulphur.

Common insect pests—same as under Mung.

Practically all plants may be called vegetables. But the term 'vegetables' is generally applied to all such edible plants whose different organs like roots, stems, leaves and fruits are eaten either cooked or raw. As sources of human carbohydrate or starchy food, vegetables stand next to cereals. The food value of vegetables is less owing to the presence of large amount of water. But the nutritive value of vegetables is quite high as they contain various types of mineral salts and vitamins.

Vegetables can be grown in succession on the same plot of land, because they are short-duration crops. In India, vegetable consumption per capita is inadequate—the production of vegetables is not even half the quantity required.

According to Hill (1952), vegetables may be classified into (a) *earth vegetables*, (b) *herbage vegetables* and (c) *fruit vegetables*.

A. EARTH VEGETABLES : These include all types in which food is stored in underground parts *e.g.* roots and underground stems like tubers, bulbs, corms, rhizomes etc. On the basis of the storage organs, earth vegetables are further classified into (1) *roots or root crops* and (2) *underground stems*.

(1) *Roots or Root Crops*—The edible portion of this group is enlarged and fleshy root which contains carbohydrate, vitamins and mineral salts. Roots or root crops include radish, carrot, turnip, beetroot, sweet potato etc.

4.1 Radish (*Mula*, *Mooli*) belongs to the family Cruciferae, the botanical name is *Raphanus sativus* L. Plant is annual or biennial herb with a fleshy fusiform tap root. Leaves are small, rosette and lyrate. Flowers large, yellow or white or lilac in long bractless racemes. Sepals erect. Petals clawed. Fruit indehiscent, elongated, terete, thick.

In India, radish is grown both in plains and in hills throughout all the states but chief centres of cultivation lie in U. P., the Punjab, Madhya Pradesh and Baroda.

Season and Cultivation—The Indian types of radish are grown from August to January while European types from September to March. Radish thrives well in free-draining loam or sandy loam soil. The land is ploughed and harrowed several times to make a mellow bed, it should be level and laid out into ridges and furrows. The soil is manured with well decomposed farmyard manure or compost at the rate of 10-20 tonnes per acre, sometimes an application of a mixture

of fertilizers containing nitrogen (18-22.5 kg.), P_2O_5 (18-22.5 kg.) and K_2O (36-45 kg.) helps in quick growth and gives higher yields. Radish is sown on ridges 45.5 cm apart. Seed, mixed with coarse sand, is sown in rows with hand at the rate of 3.38 kg. per acre and covered with soil. Immediately after sowing, one irrigation is given between the ridges, then subsequent irrigations are given after every 4 or 5 days during hot weather and 8-10 days during cold weather. Weeding operations are necessary during the early stages of growth. Thinning and spacing of plants in each row are also necessary.

Harvesting and Yield—Harvesting of Indian types of radish is generally made in about 45 days after sowing while European types are harvested in about 20 days after sowing. The average yield of Indian types varies from 4.5 to 7.2 metric tonnes per acre while that of European types varies from 3.6 to 5.4 metric tonnes per acre.

There are many varieties of radish differing mainly in size and colour of the roots. The roots are eaten raw or may be cooked.

Diseases and Insect Pests—Radish is attacked by bacterial disease known as 'soft rot'—this disease can be checked by maintaining proper drainage system. Among insect pests, attacks of aphids and painted bug (*Begrada picta*) are serious—they can be controlled by spraying with nicotine sulphate and rosin compound respectively.

4.2 Carrot (*Gajar*) belongs to the family Umbelliferae, the botanical name of which is *Daucus carota* L. Plant is biennial herb with yellowish conical type of tap root. Leaves 2-4 pinnate, segments small or narrow. Flowers white, outer often irregular in compound umbels, bracts pinnate, bracteoles many. Sepals connate in a calyx tube. Petals 5, obovate. Stamens 5, Carpels 2, connate. Fruit hirsute, elliptic, terate; ridges all prominent, secondary ridges bristly.

Carrot is cultivated throughout India—both in plains and in hills; but main centres of cultivation lie in North India (U.P., the Punjab), Maharashtra and South India.

Season and Cultivation—Carrot is grown in different times in different parts of India. In the plains of North India, native varieties of carrot are grown from the middle of August to the end of October but the European varieties are grown from September to November. In hilly tracts, carrots are grown from March to July. In South India and Maharashtra, carrot is sown in September-October.

Carrot is cultivated in a way similar to that of radish but the seed rate in case of carrot is 5.3 kg. per acre.

Harvesting and Yield—Carrots are harvested when the roots attain a diameter of 2.5-3.7 cm at the upper end. The average yield per acre varies from 4.5 metric tonnes to 9.6 metric tonnes.

There are several varieties of carrot; they differ in size, shape, colour and quality. Carrots are eaten either raw or cooked. Sometimes, yellow colouring matter 'carotene' is extracted and used for

colouring butter. Carrot is very rich in vitamin A which is synthesised from carotene.

Diseases and Insect Pests—Same as under Radish

4.3 Turnip (*Shalgam, Saljam*) belongs to the family Cruciferae, the botanical name of turnip is *Brassica rapa* L. (Syn. *B. campestris* L. var. *rapa* Hartm.). Plant is biennial herb with fleshy napiform root ; leaves are rosette.

In India, turnip is cultivated mainly in the Punjab, U. P., Maharashtra, South India. Now-a-days other states also cultivate turnip.

Season and Cultivation—The native varieties of turnip are sown from July to September while European types from October to December and even up to February in some parts. In hilly tracts, it is grown from March-May.

The method of cultivation is like that of radish but the seed rate per acre is 1.25 kg.

Harvesting and Yield—Turnips are harvested when napiforms attain a diameter of 7.6-10.2 cm. The average yield per acre varies from 6.5 to 9.0 metric tonnes.

There are mainly three varieties e.g. white, red and creamy-yellowish types. The flesh of roots varies in texture. Turnips are eaten cooked.

Diseases and Insect Pests Same as under Radish.

4.4 Beet root (*Beet, Chukandar*)—These include several varieties of a single species *Beta vulgaris* L., *B. vulgaris* forms the common garden beet and beet root while *B. vulgaris* var. *rapa* Dum. is the sugar beet. In Bengal, another variety e.g. *B. vulgaris* var. *bengalensis* Roxb. is also cultivated as beet root crops. All the plants belong to the family Chenopodiaceae.

Beet plants are biennial herbs with napiform roots. Leaves are rosette, radical and alternate, sub-entire. Flowers small, bisexual, ternate or fascicled, axillary or in terminal spikes or panicles ; bracts distinct, bracteoles 2. Perianth calycine, 5-fid. Stamens 5, perigynous, anthers oblong, 2-celled. Ovary depressed globose, half inferior. Disk thick, surrounding the base of the ovary. Ovary sub-sessile. Stigmas connate below in a style, usually 2-3. Fruit adnate below to the hardened perianth, utricle.

In India, beet roots are cultivated both in plains as well as in hills, but main centre of cultivation lies in northern India.

Season and Cultivation—Beet roots are sown from March to middle of July. They are also cultivated like radish but seed rate per acre is 9 kg.

Harvesting and Yield—Beet roots are harvested when roots attain a diameter of 5.5-7.6 cm. The average yield of beet roots per acre varies from 3.6 to 5.4 metric tonnes.

Varieties of beet roots or common beets differ in size, shape, colour, sugar content etc. Beet roots are taken either cooked or raw as salads.

Diseases and Insect Pests—Same as under Radish.

4.5 Sweet potato (*Mishti alu*, *Shakarkandi*) is the most important of all root crops. The tubers of sweet potato are edible, they are modified roots and very rich in starch. Owing to the presence of much amount of starch (20-31%), some sugar (2·8-4·4%), and even a little protein (1·2-1·8%) and fat (0·3-0·7%), the importance of sweet potato as subsidiary food to rice or wheat has been realised greatly now-a-days.

Sweet potato is a native of tropical America and East Indies. Now-a-days it is widespread in the tropics and some parts of temperate zones. In India, it is now cultivated throughout all states for the edible root tubers. All over India, sweet potato is grown both as *kharif* and *rabi* crops. In India, the area under the cultivation of sweet potato is extensive although accurate statistical figures of acreage in different states are not available.

Botanically sweet potato is known as *Ipomoea batatas* (L.) Poir. belonging to the family Convolvulaceae. Plant is a prostrate herb, normally creeper and develops adventitious roots at the nodes. The adventitious roots form a root system and some of them due to storage of reserve food, swell up forming tubers which are more or less *fusiform* in shape. The length of stem varies from 5 to 50 cm : fresh vines i.e. stems are variously coloured e.g. green, purple or a combination of purple, brown and green. Leaves are simple and alternate, petioled ; there is variation in the form, shape, size and lobation of leaf lamina.

Flowers¹, when present, are coloured which vary in shades of red and pink, turning darker near the corolla throat. Sepals 5, ovate or linear. Petals 5, connate in a campanulate or funnel-shaped corolla, limb plicate. Stamens 5, included. Carpels connate in 1-3 or 4-celled ovary. Style filiform, stigma capitate. Fruit a 4 to 6 valved capsule. Seeds 4 or 6, rarely 1 ; glabrous.

Climate—Sweet potato is a warm season crop, it requires high temperature for best growth. Under proper conditions, the tubers can be kept in store for few months.

Season and Cultivation—Sweet potato is propagated vegetatively either by vine-cuttings from vines of previous season or from sprouts produced on the tubers. Transplanting of vine-cuttings is done towards the end of April-May or in some cases from September to November. The land should be either high land or on a gentle slope. The best soil for sweet potato cultivation should be either sand or sandy loam. One ploughing and one cross ploughing followed by one grubbing should be given—this may be followed by

¹ Normally, sweet potato does not produce flowers—this is due to the continuous propagations by vegetative means.

one or two harrowings to remove the weeds and then one laddering to make the land to a level. The land should be made into ridges 30.5 cm high and 91.4 cm apart. Normally the land is not manured; when manuring is necessary, the land may be manured with green manures like '*dhaincha*' or sunn-hemp (*Crotalaria juncea*); in case of chemical fertilizers, 181.0-453.0 kg. of 3 : 8 : 6 or 4 : 8 : 6 of N, P, K per acre may be used. Vine-cuttings, 30.4-45.7 cm long, are planted 30.5 cm apart in rows at 45.5-60.8 cm distance. Immediately after planting the field should be watered.

Harvesting and Yield—The crop matures in six months. At the end of this period a general browning off of the leaves is seen which indicate that the crop is ready for harvesting. The vines are first removed by cutting and then the tubers are dug up with the help of a forked *kodali*.

The average yield of indigenous variety varies from 3.6-4.5 metric tonnes per acre. But some of the varieties (e.g. Tie Shin Tun) yield over 16.5 metric tonnes per acre.

Uses—Sweet potatoes are used as food either boiled or roasted. They are also used for canning, dehydrating, flour manufacture and as a source of starch, glucose, syrup and alcohol. They are also used in making some kind of sweetmeat. In foreign countries, the tubers are fed to horses, cattle and pig. Leaves and green vine tops are used as fodder.

Varieties—There are several varieties of sweet potato e.g. (1) *Pusa*, (2) *Anakapalle*, (3) *Jhungania*, (4) *Bengal white*, (5) *Bengal purple*, (6) *Rangar*, (7) *Pusa lal*, (8) *Pusa safed*, (9) *Pamna* etc. These varieties differ from each other in several character like (a) length of vines, (b) thickness of stems and number of branches, (c) colour and nature of stem, (d) length of petiole, (e) lobation of lamina, (f) skin colour of roots, (g) flesh colour and (h) surface of tubers. All the varieties may be divided into two groups viz, (1) the dry mealy type and (2) watery, soft, gelatinous fleshy type rich in sugar.

Diseases and Insect Pests—Common diseases are—Leaf spot caused by *Cercospora batatae*—can be controlled by spraying with 10% Bordeaux mixture; Charcoal rot and Soft rot caused by *Macrophomina phaseoli* and *Rhizopus nigricans*—these can be controlled by raising vines from tubers growing in disease free area and avoiding brushing tuber at harvesting respectively. Sweet potato is attacked by pests known as sweet potato weevil and sweet potato sphinx, they attack roots and stem. They can be controlled by spraying 0.25% DDT on the under-side of the leaves. Use of plants free from insect infestation, clearing up the fields and storage house etc. are the methods of control.

(2) **Underground Stems**—The edible portion of this group is enlarged and fleshy underground stems usually storing up carbohydrate food materials. It includes tubers, corms, bulbs, rhizomes etc.

4.6 Potato (*Alu*, *Aaloo*) is one of the most important and common food plants of the world. The edible portions are the tubers which are modified stems rich in carbohydrates; potato contains 78% water, 18% carbohydrates (starch), 2% proteins, 0.1% fat and 1% potash and a little sugar. Potato is essentially a crop of cool and moist regions.

Potato plant is a native of S. America, it was introduced into Europe by the Spaniards in 1580 and it then gradually spread all over Europe and the British Isles by the end of the seventeenth century. In India, potato is cultivated throughout all states, both in plains as well as in hills.

Botanically potato is known as *Solanum tuberosum* L. belonging to the family Solanaceae. Plant is an erect, branched, more or less spreading annual herb up to 0.9 m in height. Leaves are pinnately compound. Flowers are white, purple or yellow in racemose inflorescence. Sepals connate in a 5.6 lobed calyx. Petals usually 5, connate in a rotate corolla. Stamens 5, epipetalous, filaments short, anthers oblong, narrowed upwards opening by terminal pores. Carpels 2, connate in 2-4 celled ovary. Style columnar, stigma small. Fruit is small brownish-green or purple globose berry. Seeds many, discoid.

Season and Cultivation—Potato is a cold season crop, it grows well in moist regions where the temperature is low *i.e.* not exceeding above 21°C. A loam or sandy loam soil is usually preferred for better growth. In plains, the main potato crop is sown in September-October, but in the higher hills potato is sown from March-April while in the lower hills, it is normally grown during December-January. Sometimes two varieties (early and late) are grown on the same land, in this case planting for early crop is done during September while the second crop is planted during December just after the first crop is harvested.

The land should be ploughed and re-ploughed until it is broken into fine dust, then it is levelled by laddering and laid out into ridges and furrows. Before planting, a dose of fertilizer mixture to supply 22.5-45.3 kg. N, 22.5-31.6 kg. P_2O_5 and 45.3-67.9 kg K_2O per acre may be given in furrows.

Potato is propagated by planting either cut or whole tubers. In the hills, cut tubers having 2 or 3 eyes are generally sown while in plains, both cut tubers (in case of spring crop) and whole tubers (for main *i.e.* autumn crop) are sown. The seed rate for the main crop of plains, when whole tubers are planted, varies from 362.5 to 453.0 kg. per acre : but the seed rate for the crop of hills and spring crop of plains, when cut tubers are planted, varies from 453.0 to 543.6 kg. per acre. Seed potatoes are planted in furrows, 45.6 cm apart ; in each furrow seed potato is planted 10-22.5 cm apart. Then the field is planked to cover the seed potatoes and to level up the ridges. Irrigation should be given at intervals of 7-10 days. In case of a deficiency in nitrogen, one or more top dressings of 9.0-14.5 kg. N per acre may be given at each earthing up.

Harvesting and Yield—Potatoes mature in three months from the time of planting. Potatoes are ready for harvest when the tubers do not peel off easily. With the help of a forked *kodali*, tubers are dug up. Depending on the season of cultivation and the variety grown, the yield of potato varies from 3.6-9.6 metric tonnes per acre.

Uses—Potatoes are mainly used as food, either boiled or roasted. Small tubers are also used for the production of starch and industrial alcohol, they are also fed to stock.

Varieties : Though there were several varieties in existence, several high yielding and disease resistant varieties have been released by the C. P. R. I. Simla. Important among these are : (i) Kufri Sinduri, (ii) K. Chandramukhi, (iii) Kufri Kissan, (iv) K. Chamatkar etc. In West Bengal, Achersegen, Up-to-date, R.K.M., K. Chandramukhi, K. Sinduri are among the recommended potato varieties.

Diseases and Insect Pests—The potato crop suffers from the following diseases :—

(a) *Early blight* caused by *Alternaria solani*—can be controlled by thorough spraying with Bordeaux mixture. (b) *Late blight* caused by *Phytophthora infestans*—can be controlled by spraying with Bordeaux mixture and other fungicides. (c) *Ring* or '*bangle*' disease caused by *Pseudomonas solanacearum* (bacteria)—can be controlled by using disease free seed tubers and through rotation with cereal crops. (d) *Mosaic Virus* disease—can be controlled by using disease free seed tubers.

Among insect pests, cut worms and potato moth are injurious, they can be controlled by dusting with 5% BHC or DDT powder.

4.7 Onion (*Piaj*, *Piaz*) forms one of the most important and common bulb crops of the world. In this plant, food is stored in the bulb which consists of the swollen bases of green foliage leaves and fleshy scales.

The use of onion as vegetable is very old, perhaps going back over 4,000 years beyond the beginning of authentic history. It is probably a native of southern Asia or Mediterranean region. In India, onion has long been valued for its flavouring and is cultivated all over the country.

Onion is botanically known as *Allium cepa* L. belonging to the family Liliaceae¹. Plant is biennial herb with a single large bulb and long, hollow cylindrical leaves. Flowers are small and numerous, borne on a single leafless scape and in umbel-like cymes. Bracts membranous, 2–3. Perianth of 6 segments, sub-calyceine. Stamens 6, filaments free, filiform or \pm dilated below. Carpels 3, connate in a 3-celled superior ovary. Fruit a membranous loculicidal capsule.

Season and Cultivation—Onion is mainly a mild season crop though it can be grown in varied climatic conditions. Onion is grown during winter and harvested before the beginning of summer. It is propagated primarily through seeds, besides propagation through setts (produced by sowing seeds) and small bulblets produced by plants instead of flowers are also common. The nature of the soil and the preparation of land for the cultivation of onion are the same like that of other vegetables. Onion seed is sown broadcast at the rate of 3.5-4.5 kg. per acre from September to November and transplanting at distance of 7.5-10.0 cm in rows 22.8-30.4 cm apart is done in the field during December–January. Transplanting is followed immediately by irrigation. Before planting, a fertilizer mixture may be applied to supply 22.5 kg. N, 22.5 kg. P_2O_5 and 45.3 kg. K_2O per

¹ The genus *Allium* is at present placed under the family Alliaceae—intermediate between Liliaceae and Amaryllidaceae,—in having superior ovary and umbellate inflorescence.

acre. A side dressing of 22.5 kg. N, may be given one month after sowing. Where the crop is raised from setts or bulblets, these setts or bulblets are pulled out in the beginning of August and then re-planted in September to raise the main crop in December.

Harvesting and Yield—Onion is harvested before the beginning of hot season when the leaves have turned yellow and the tops have fallen over. The average yield of onion per acre varies from 2.6 to 10.8 metric tonnes.

Uses—From the standpoint of food value, onion is not important but is used for flavouring vegetables and meat dishes. It is also used for making salads, pickles etc.

Diseases and Insect Pests—Onion crop is attacked sometimes by a fungal disease known as *blight* caused by *Alternaria solani*—it can be controlled by spraying with Bordeaux mixture and by observing sanitation.

The common insect pest is *Thrips tabacii*, the attack of this pest can be controlled by spraying with DDT or dusting with 5% BHC at 11.3 kg. per acre at the intervals of seven days.

B. HERBAGE VEGETABLES—These include plants in which nutrient materials are stored in aerial parts of plants. Pot herbs, salad plants, cole crops like cabbage, cauliflower, knolkhol or kohlrabi etc. are the examples of familiar herbage vegetables.

4.8 Cauliflower or Broccoli (*Fulkapi, Phool gobhy*) is mainly a cold season crop and can withstand considerable frost. Cauliflower is mainly cultivated all over northern India, it is also grown in various parts of West Bengal and Assam. The entire immature inflorescence of abortive flowers forms a large head which is edible. Cauliflowers are eaten cooked.

The botanical name of cauliflower is *Brassica oleracea* L. var. *botrytis* L. belonging to the family Cruciferae. Plant is biennial herb having a short erect stem. Leaves are simple, alternate, lyrate, and large, often tied around the mass of flowers. Flowers in raceme but aggregated to form a globose head-like structure on thick hypertrophied branches.

Season and Cultivation—Cauliflowers are produced by transplanting seedlings which are raised in seed-beds. They grow well in loamy soil, the soil of the seed bed is well ploughed and manured with oil-cake, cowdung, ammonium sulphate and superphosphate. Seeds are sown by broadcast at the rate of 0.42 kg. per acre from March to July in hills and in plains from June to August (for early variety) or from September to October (for late variety). Seedlings are transplanted in well prepared land in rows in 5.0-6.5 cm apart and 38.0-45.5 cm in row. A week or two before transplanting, a mixture of fertilizers may be applied to the soil to supply 36-45.5 kg N, 36.5 kg. P_2O_5 and 45.5-67.9 kg. K_2O per acre. Then watering is done every 10-14 days. Weeding and hoeing operations should be continued till the leaves cover the soil. A top dressing of 18.0-22.6 kg. N may be given about 6 weeks after transplantation.

Harvesting and Yield—Cauliflower matures within 2-4 months from the time of planting. They are ready for harvest when the heads become creamy white in colour and before they break open. The average yield varies from 20 to 30 tonnes per hectare.

Some of the important varieties of cauliflower are :

Early : Early Patna, Kunwari, Pusa katki.

Mid. Season : Aghani, Poosi, Patna, Early snowball, Giant snowball.

Late : Dauia, Snowball-16, Sutton's snowball.

4.9 Cabbage (*Bandha kapi*, *Patgobhy*) is another important garden crop in cool climates. It is one of the oldest garden crop and was introduced in England by the Romans. Cabbage contains 91% water together with some sugar and starch, little protein and valuable calcium salts. It is rich in vitamins A, B₁, B₂, and C. Cabbage is grown for its enlarged terminal buds which are eaten raw or cooked. In Europe, it is also used for feeding stock and chickens.

In India, cabbage is cultivated as a winter crop throughout all states although extensive cultivation takes place in N. India.

The botanical name of cabbage is *Brassica oleracea* L. var. *Capitata* L., belonging to the family Cruciferae. Plant is biennial herb ; stem is short, stout but delicate bearing overlapping leaves.

Season and Cultivation—Cabbage is sown from August to November, the amount of seeds required to produce seedlings for one hectare varies between 375 and 500 gms. Like cauliflower, cabbage is also produced by transplanting seedlings that are raised in nursery beds. Cultivation is like that of cauliflower.

Some of the varieties commonly grown in India are : Chieftain, Golden Acre, Mammoth Rock Red, Pride of India, Pusa Drum head.

4.10 Knolkhol or Kohlrabi (*Olkapi*, *Ganth gobhy*) : It also belongs to the family Cruciferae, the botanical name of which is *Brassica oleracea* L. var *gongylodes*. L. In knolkhol, no head is formed but the short stem is transformed into an enlarged and juicy mass of edible tissue forming a structure what is known as *ganth gobhy* or *olkapi*.

Knolkhol is spherical and turnip-like, either white or purple in colour with prominent leaf scars. Plant is a biennial herb with rosette of long petioled leaves. It is used for human food and generally eaten cooked. In India, extensive cultivation takes place in the Punjab, Baroda, Maharashtra and U. P.

Season and Cultivation—Knolkhol is a cold season crop. Seeds are sown by drilling from August to October or November at the rate of 1.0-1.5 kg. per hectare and the seedlings are transplanted in a well ploughed and manured loamy soil in rows 30 cm apart and plants spaced 20 cm in row. Application of fertilizer mixture, irrigation and dressing of the land are done in a similar way as in case of cauliflower.

Harvesting and Yield—Knolkhol matures within 1-1½ months after transplanting. They are harvested before they become fibrous. The average yield per hectare varies from 20-25 tonnes.

Two varieties are commonly grown in India, viz. White Vienna and Purple Vienna.

Diseases and Insect Pests of Cabbage, Cauliflower and Knolkhol. Damping off (caused by *Pythium debaryanum*), Club root (caused by *Plasmiodiophora brassicae*), Leaf spots and blight (caused by *Alternaria brassiciola*), Black rot (caused by *Xanthomonas campestris*) etc. are the diseases of the above mentioned cole crops. These diseases can be controlled by avoiding over watering, avoiding infected fields and treating seedlings with mercuric chloride solution at the time of transplanting, spraying with 1% Bordeaux mixture and hot water treatment of seeds at 50°C for half an hour, rotation with non-cruciferous crops respectively.

Important insect pests are cabbage butterfly, tobacco caterpillar, mustard sawfly and diamond-back moth—all these can be controlled by spraying with DDT (36 grams in 27 litres of water).

C. FRUIT VEGETABLES—These include all fruits which are generally not taken in the raw state and require cooking, therefore fruit vegetables are used as vegetables rather than fruits. In India, various types of fruit vegetables are cultivated, of which cucurbitaceous crops i.e. cucumbers, pumpkins, gourds, squashes etc. and others like brinjal, okra (bhindi or lady's finger), tomato etc. are important.

4.11 Cucumber (*Shasha*, *Kheera*), Pumpkin or gourd (*Kumra* or *Sita phal*), Patal or Pointed gourd (*Patal*, *Palwal* or *Parwal*), Bottle gourd (*Lau* or *Lauki*) etc.

All the above mentioned crops belong to the family Cucurbitaceae, hence they are also known as *cucurbitaceous crops*. They are hot season crops. Botanically cucumber is known as *Cucumis sativus* L., pumpkin as *Cucurbita pepo* L., patal as *Trichosanthes dioica* Roxb., and bottle gourd as *Lagenaria siceraria* (Mol.) Standl. (Syn. *L. vulgaris* Serin).

Plants are herbs or shrubs, mostly tendril climbers. Leaves simple, alternate, petioled; leaf blade lobed or entire. Flowers regular, epigynous, unisexual, pentamerous. Stamens 5, connate, forming synandrium. Carpels 3, ovary inferior. Placentation parietal, ovules many. Fruit fleshy, berry-like or pepo.

The fruits (specially unripe and tender types) of all these crops are cooked as vegetables; although they contain much amount of water, still they are good source of vitamins.

Most of the cucurbitaceous crops are cultivated all over India except 'patal' which is not grown in north-west India. Cucumber, pumpkin, bottle gourd etc. are propagated from seeds whereas 'patal' or pointed gourd can also be propagated from root cuttings besides from seeds.

Season and Cultivation—In the plains seed is sown from January to March whereas in the hills from April to July. The seed rates per hectare are 2.5 kg. for cucumber, 7-8 kg. for pumpkin, 4-5 kg. for bottle gourd and 6.7-9.0 kg. for patal or from cuttings. The seeds may either be sown broadcast in loamy, clayey or sandy loam soils (for patal) or planted near the edge of raised beds having furrows in between them to facilitate watering. The width of bed varies—for cucumber, it is 1.5 m; 2.4 m for bottle gourd and patal,

and 3.0-3.6 cm for pumpkin. In the hills, seeds are sown 0.6-0.9 m apart; 3-4 seeds are planted about 19.0 mm deep in each hill. Immediately after sowing, irrigation is given. In hot weather, the crop is watered every third or fourth day. Frequent weeding is necessary. Before sowing, the soils may be manured with a fertilizer mixture containing 22.5 kg. N, 22.5 kg. P_2O_5 and 45.3 kg. K_2O .

Harvesting and Yield—For immediate use, the fruits of all these crops are harvested when they are still tender. For storage, they (specially pumpkin) are harvested in fully ripe stage. The average yield per hectare for these crops are :—cucumber 8-10 metric tonnes, patal 12-15 metric tonnes, pumpkin 25 metric tonnes and bottle gourd 15-20 metric tonnes.

Diseases and Insect Pests—Cucurbitaceous crops are mainly attacked by fungal disease known as downy mildew and powdery mildew. The damage is done to the leaves. These diseases may be controlled by thorough dusting with fine sulphur and spraying with 1% Bordeaux mixture.

Red pumpkin beetle is the most serious insect pest, it does the maximum damage to the seedlings. The attack of this pest may be controlled by spraying 0.1% Lindane or dusting Lindane dust on the plants.

4.12 Tomato (*Bilati begun*, *Tamatter*) and Brinjal or Egg-plant (*Begun*, *Baigon*): These two fruit vegetables belong to the family Solanaceae. Botanical name of tomato is *Lycopersicon esculentum* Mill, and of brinjal is *Solanum melongena* L. Both are warm season crops and susceptible to cold.

Brinjal is a native of India, it is cultivated throughout India. Tomato is a native of S. America, now it is cultivated everywhere and it ranks next to potatoes and sweet potatoes in importance. Tomato and brinjal are of high nutritive value and contain vitamins A, B, C and A, B respectively. Tomatoes are eaten both raw and cooked, pulp is used in canning; the ripe tomatoes are also used for sauce, ketchup, tomato juice, tomato pastes etc. but green *i.e.* unripe tomatoes are used for pickles and preserves. Brinjals are taken cooked or fried as a vegetables.

Tomato plant is a tall branched herb, either trailing or erect. Leaves pinnate, pinnae lyrate or toothed. Flowers in cymes. Sepals connate in a 5 or 6 partite calyx, petals 5, rarely 6, connate in a rotate corolla. Stamens 5 or 6, epipetalous, anthers dehiscent by longitudinal slits. Carpels 2, connate in a 2-4 celled ovary. Fruit a fleshy berry; embryo curved.

Brinjal plant is a stout herb, unarmed or prickly. Leaves simple, alternate or sub-opposite, entire or lobed. Flowers blue, in lateral or terminal cymes. Sepals 5-10 lobed, connate; petals 5 or 4-6, connate in a rotate corolla. Stamens 5 or 4-6, anthers dehiscent by apical pores; other characters like tomato plant.

Season and Cultivation—Seeds of tomato and brinjal are small and very light; they are generally sown in nursery bed from June to November for producing transplants. In the hills, for raising transplants, seeds are sown from March to May. In northern India,

generally three crops are taken during the year—for the first crop, seed is sown for raising transplants from middle of June to end of July; for the second crop from middle of August to middle of October and for the third crop from middle of October to November. About 56.5-85.0 grams of seeds are sown in rows 7.6 cm apart over one *marla* (272 sq. ft.). About 400-500 gms. of seeds are required for one hectare of land. Within 4-6 weeks, seedlings become ready for transplanting. The seed bed is provided with shade during hot weather.

The seedlings are planted in the well prepared field in rows 0.6-0.9 m apart and at distance of 38.0-45.6 cm in the row. Immediately after transplanting, irrigation is given and thereafter every week. Frequent hoeing is necessary to keep the weeds in check. For tomatoes, staking is required when the plants attain a height of 22.8-30.4 cm. Just before sowing or planting a fertilizer mixture containing 18.0-22.6 kg. N, 22.6-36.0 kg. P_2O_5 and 45.3-54.3 kg. K_2O may be applied.

Harvesting and Yield—Brinjals are harvested when they attain full size but before they are fully ripe. Tomatoes are harvested either at ripe stage for table use or at green stage for the use as vegetables. The average yield per acre for brinjals is 20-25 metric tonnes and for tomatoes 16-20 metric tonnes.

Diseases and Insect Pests—Common diseases of tomato are leaf curl, leaf mould, mosaic and leaf vein caused by viruses—these diseases can be controlled by spraying with nicotine sulphate, soap solution and DDT or lime sulphur respectively. Tomato plants also suffer from early blight, late blight, damping off, fusarium wilt diseases—these can be controlled by weekly spraying with 3 : 3 : 50 Bordeaux mixture. Important diseases of brinjal are damping off, phomopsis blight, wilt, sclerotium, mosaic little leaf etc.

Among insect pests, epilachna beetle and tomato fruit worm on tomato and red mite, shoot & fruit borer, epilachna beetle on brinjal plants are the most serious types—tomato fruit worm can be controlled by spraying with 0.1% DDT at fortnight intervals, epilachna beetle can be controlled by spraying 5% DDT dust @ 15-20 lb. per acre or 0.1% DDT @ 50-100 gallons per acre.

Varieties : Some of the important varieties of tomato and brinjal grown in India are :—

Tomato : Marglobe, Ox-heart, Ponderosa, Best of All, Fireball, Pusa Early Dwarf, Pusa Ruby, Sioux.

Brinjal : Banaras Giant, Black Beauty, Muktakeshi, Pusa Purple Long, Pusa Purple Round, Wynad Giant.

Fruit is the seed bearing mature portion of the flower *i.e.* ovary. Fruit develops mainly from the ovary alone but sometimes other accessory structures of the flower such as calyx and receptacle are also involved in the formation of fruit. Fruits may be simple or compound and dry or fleshy. Some of the dry and fleshy fruits used as grains and vegetables have already been discussed in preceeding chapters. In this chapter we will consider only those fruits which are usually *eaten without cooking*—hence the term ‘fruit’ is applicable only to those fruits taken raw in common usage. In India, great number of both temperate and tropical fruits are cultivated. The tropical fruits have great nutritive value in comparison to temperate fruits. Various types of organic acids like malic, citric, tartaric etc., mineral salts and vitamins are present. Carbohydrates are abundant, fats and proteins are negligible; water content varies from 70-80%. The area under fruit crops in India is slightly over 3 million acres or about 0.8% of the total cultivated area.

5.1 Banana, Plantain (*Paka Kala, Kela*): It is one of the most familiar and important of all tropical fruits. Banana is a native of the tropics of India and Malaya from where it has spread all over the tropical world. It is believed to be the world’s oldest cultivated fruit crop.

In India, banana occupies over 1,85,000 hectares and is cultivated mainly in Assam, West Bengal, Bihar, Madhya Pradesh, U.P., Maharashtra, Madras, Andhra Pradesh, Kerala, Mysore and Gujrat. Banana is a moist, heat loving plant and susceptible to frost or arid conditions.

Botanically banana is known as *Musa paradisiaca* L. (Syn. *M. sapientum* L.) belonging to the family Musaceae. Plant is tall herb with rhizome; the pseudostem developing from rhizome and ending in inflorescence in surrounded by large leaf sheaths. Leaves are very large, forming a crown, oblong, deep green and each is provided with a prominent midrib. Inflorescence pendulous, mixed spadix, bracts large—spath-like, ovate or boat-shaped subtending many to few flowers at their axils and are arranged in cyme. Flowers are mostly bisexual, rarely unisexual by abortion, epigynous, white, greenish or yellowish. Perianth segments 6, of which 5 are united to form a 5-toothed perigonium. Stamens 5. Carpels 3, connate; ovary inferior, 3-celled; placentation axile. Fruit fleshy berry, seedless or seeded.

Propagation and Cultivation—Banana is propagated vegetatively by suckers or offshoots developing at the base of the plant from

underground rhizomes. Healthy suckers having a stout base together with a piece of rhizome with roots and tapering top with few narrow leaves are selected for planting. Suckers are generally planted during rainy season, although they can be planted throughout the year except during summer.

The field is cleared thoroughly first and then ploughed properly. Then, suckers are planted in small pits, the distance varies from $2\text{m} \times 2\text{m}$ (for dwarf varieties) to $4\text{m} \times 4\text{m}$ (for tall varieties). At the time of planting, 20-25 kg. farmyard manure together with 5 kg. wood ash may be applied to each plant. Later, a complete fertilizer mixture may be applied to the field to supply 100-200 kg. N, 100-200 kg. P_2O_5 and 200-400 kg. K_2O per hectare.

Next, after-care operations are very important, this operation includes the removal of unwanted suckers, dry leaves and pseudo-stems from which fruits have been harvested. Weeding operations are also needed either by hand or by hoe and harrow or by the application of chemical weed killers. At the time of the formation of fruit bunches, propping of plants with bamboo poles is necessary.

Banana requires large amounts of water. But water logging is detrimental. After the rainy season irrigation is necessary every fortnight or 10 days and even every 5-8 days during March to May.

Harvesting and Yield—Early varieties produce flowers in seven months after planting and the fruits take three months more to ripen. Fruits of late varieties mature in 12–14 months after planting. When the fruits attain full size and become plump and mature just before the ripening stage, then the fruit bunch is harvested. Sometimes the bunch may be harvested earlier for long transport. At the time of harvest, the bunch is carefully cut retaining about 15 cm of the stem above the first hand. The yield per hectare varies from 26-35 metric tonnes.

Ripening of Banana—Generally, banana is harvested raw and then ripened artificially. It is done in various ways e.g., wrapping banana with green leaves and piling them in heap, placing the bunches over a hearth, exposing to sun, storing in closed and airtight godowns or smoking them. Within 30-48 hours, ripening of fruits takes place.

Uses—The ripe fruits are edible and delicious to taste, they constitute one of the most healthful and nourishing foods. The green fruits are also used as vegetables. The leaves are commonly used as plates. Banana flour, made from dried green fruits are used in the manufacture of chocolate and biscuits. The unripe fruit and the inner core of the pseudostem (*thor*) are cooked as vegetables. In Bengal the end of the inflorescence (*mocha*) is also eaten as vegetable curry. Banana contains very little water and the ripe fruit is a fair source of vitamins A, B_1 , B_2 and C and contains up to 27% sugars. It is also rich in magnesium, sodium, potassium, phosphorus and contains fair amounts of calcium and iron.

Diseases and Insect Pests—Common and important diseases are : (a) Shoot rot caused by *Ceratostomella paradoxa* ; (b) Wilt caused by *Fusarium oxysporum*—it can be controlled by eradicating affected plants, applying crude oil to rhizome, treating soil with nematicide etc. ; (c) Anthracnose caused by *Gloeosporium musarum*, can be controlled by spraying with 1% Bordeaux mixture ; (d) Black finger caused by *Macrophoma musae*—can be controlled by removing affected fingers and spraying with 1% Bordeaux mixture ; (e) Main stalk and finger stalk rot caused by *Botryodiplodia* spp. and *Gloeosporium* spp.—can be controlled by cutting the main stalk well above and dusting some fungicide to the cut end of the stalk, then a piece of grease proof paper should be tied, or by treating the bunch at a lower temperature (20-25°C) ; (f) Bunchy top and mosaic viruses—can be controlled by selecting healthy suckers for planting and controlling aphid vector with insecticides.

Common insect pests are :—(a) Weevil borer (*Cosmopolites sordidus*)—it can be controlled by spraying with 0.10% DDT around the base of the plants @ 225-330 litres per acre, by selecting insect free rhizomes for planting. (b) Stem borer, (*Odoiporus longicollis*)—can be controlled by up-rooting and burning infested plants.

Varieties—Cultivated types are mainly divided into two groups, viz. (a) *table* and (b) *culinary*. Table group includes several varieties like *Champa*, *Mortaman*, *Kanthali*, *Amrit Sagar*, *Poovan*, *Ney poovan*, *Pacha nadan*, *Basrai* etc. Culinary group includes *Nendran*, *Monthan*, *Pacha montha bathis* etc.

5.2 Mango (Am, Aam): Mango is another most important and oldest known of tropical fruits. It is a native of southern Asia, now it is grown widely in Malaya, Polynesia, Africa and tropical America. Mango has been cultivated in southern Asia for nearly 6,000 years.

In India, mango is grown extensively in Assam, West Bengal, Bihar, Madras, Andhra Pradesh, U. P., Maharashtra and the Punjab—both in plains and hills up to about 1,500 metres ; it occupies over 5.3 lakh hectares or about half the total area under fruit cultivation in India. Mango can withstand both dry and rainfall conditions.

Mangifera indica L. is the botanical name of mango, it belongs to the family Anacardiaceae.

Plant is a beautiful evergreen tree with resin and gum passages and cells, growing up to 27.5 m in height. Leaves are simple, alternate, exstipulate, pulvinus. Flowers are small, pink, bisexual, regular, hypogynous in cymose panicles. Extrastaminal disc is present. Sepals and petals 5, imbricate. Stamen 1, perfect or fertile ; rest 4 sterile. Carpel one, ovary one celled and one ovuled. Fruit is a fleshy drupe with a thick epicarp and a large seed.

Propagation and Cultivation—Mango is propagated vegetatively either by inarching or by budding *in situ* in nursery—two methods are employed in this practice e.g. (a) “T” method and (b) *Forkert method*. Beginning of monsoon (in low rainfall areas) and end of monsoon (in heavy rainfall areas) are the best periods for inarching or budding and also for planting. Grafted plants are transplanted in the field after 5-12 months. Normally straight-growing grafts are selected and placed in pits filled with soil mixed with 45 kg. farmyard manure and fertilizer mixture containing 0.22 kg. N, 0.45 kg. P and 0.22 kg. K per pit. Planting distance varies from 7.5-9 m in shallow

poor soils and 15-17 m in deep fertile soils. Care should be taken so that graft joint remain 15 cm. above the ground. Mango may also be grown from seedlings.

Removal of dead wood and flowers appearing during the first 3-4 years and thinning of overcrowded branches after four years are necessary.

Before planting, the field should be well ploughed and harrowed—at least twice a year, once in the beginning of monsoon and other at the end of monsoon or in cold weather. Green manuring is necessary once every two or three years. Young plants have to be irrigated regularly. The adult tree should be manured regularly, the recommended dose is 45-70 kg. farmyard manure, 0.5-0.7 kg. N, 0.7-1.0 kg. P, and 1.2-1.5 kg. K per tree.

Grafted mango trees begin to produce fruits from the fourth or fifth year onwards.

Harvesting and Yield—Fruits mature within 5—6 months. Depending upon the varieties and the onset of flowering, harvesting of mature fruits begins from April-May in West India, April-July in South India and June to August in North India. Harvested fruits, after packing in baskets and properly padded with straw or green leaves, are transported to long distance. The yield per grafted tree varies considerably with the variety, vigour of growth, flowering etc. A tree normally yields about 300-500 fruits in its 10th year, about 800-1,000 in 15th year and 2,000-5,000 from 20th year onwards.

Uses—The fruits are very delicious to taste. The pulp of the ripe fruit is orange, yellow or red in colour and has a aromatic flavor with a blending of sweetness and a little acidity. The young unripe fruits are also used for making jams and pickles.

Varieties: There are over 1,000 varieties of mango in India. Some of the important varieties are—

Andhra Pradesh: Bangaupalli, Mulgoba, Suvarnarekha.

Bengal: Bombai, Fazli, Himsagar, Langra, Shadullah.

Bihar: Bombai, Fazli, Gulabkhas, Himsagar, Krishanbhog, Sukul.

U. P. & Punjab: Bombay Green, Dasherri Khajri, Langra, Gulabkhas, Krishanbhog.

Western India: Alphonso, Borsha, Jama'ar, Fernandin, Pairi, Salebhoy Airdi.

Madras: Bangalore, Neelum, Rumani.

Diseases and Insect Pests—*Common diseases of mango are*: (a) Canker and dieback diseases—can be controlled by pruning diseased branches and spraying with 1% Bordeaux mixture. (b) Sooty mould caused by *Capnodium ramosum*—can be controlled by spraying with oil resin soap (42 kg. in 27 litres of water) or crude oil emulsion (42 kg. in 27 litres of water) followed by starch solution or Folidol, Ekatox etc. (93.2 gms. in 112 litres of water). (c) Anthracnose caused by *Colletotrichum gloeosporides*—can be controlled by spraying young fruits with 1% Bordeaux mixture. (d) Powdery mildew caused by *Oidium mangiferae*—can be controlled by dusting inflorescence with sulphur.

Common insect pests are: (a) Mangooppers (*Idiocerus* spp.)—can be controlled by avoiding damp and water logging conditions in mango orchards and spraying with 0.25% DDT in spring when infestations take place. (b) Mango stem

borer (*Batocera* spp.)—can be controlled by fumigating holes and tunnels with petrol or ED/CI¹ mixture. (c) Mango mealy bug (*Drosicha mangiferae*)—can be controlled by applying sticking bands round trunks of trees in cold weather and by spraying with 0.06% Malathion or 0.05% Parathion @ 5-22.5 litres per grafted tree. (d) Mango shoot gall maker (*Apsylla cistellata*) and (e) Leaf gall makers (*Procontarinia mattheiana*)—can be controlled by destroying or burning galls and affected leaves. (f) Red ant (*Oecophylla amaragdina*)—control measures are burning and destroying the nests or spraying 0.25% BHC on the nests.

5.3 Oranges : Oranges are of three types viz., (a) sweet orange i.e. *mosambi* or *Mausmee* obtained from *Citrus sinensis* (L.) Osbeck, (b) mandarin or santra orange i.e. *kamala lebu* or *Santra* obtained from *Citrus reticulata* Blanco and (c) sour orange i.e. *khatta* orange obtained from *Citrus aurantium* L. All species belong to the family Rutaceae. Oranges have high nutritive value, they contain sugar (5-10%), citric acid (1-2%) and vitamin C.

(a) SWEET ORANGE is a native of South-eastern Asia possibly China or Cochin China. Plant is a small evergreen tree with slender blunt spines, reaching a height up to 6.0 m. Leaves gland dotted, alternate, exstipulate, evergreen with narrow winged petioles. Flowers bisexual, white, very fragrant. Stamens numerous, inserted outside the large disc. Ovary many celled. Fruit large, more or less round, berry like, with an abundant sweet, solid pulp-like and spindle-shaped juice sacs.

In India, sweet orange is cultivated in the Punjab, Rajasthan, Maharashtra, Deccan, U.P. and Madras. It is normally grown under tropical and sub-tropical conditions. Sweet orange may be cultivated on both heavy clayey and light sandy soils.

Sweet oranges are mainly cultivated for fresh edible fruits. Orange oil obtained from peel is used in the soap and perfume industry.

(b) MANDARIN OR SANTRA ORANGE is a native of China. Plant is small tree with spines, fruits rounded and smaller—other characters are like that of sweet orange.

In India, mandarin orange is cultivated in the hills of Assam (Khasia, Jaintia, Lushai hills), West Bengal (Darjeeling), Garhwal, swamps of Dehra Dun (U. P.), Sikkim, Tripura, Sirmur (H. P.), sub-montane districts of the Punjab, Coorg, Wynad tract and the Nilgiris of the South, region around Nagpur of Maharashtra etc.

Sweet orange grows in all tropical and sub-tropical climates, it tolerates more humidity in summer and winter. Sweet orange grows best on medium or light loam with little heavier sub-soil, it can also be grown on heavy black, sandy or gravelly soils.

Propagation and Cultivation—Propagation is done mainly by seed although some varieties (*Nagpur*, *Emperor* etc.) are propagated by budding. Due to polyembryonic nature of seeds, the sexual seedlings produced from the cells of the nucellus are only allowed to grow while propagating by seed. In case of budded plants, no difficulties arise. Different varieties are budded on different rootstock e.g. santra orange is normally budded on rough lemon rootstock.

In the hills, the land is properly terraced and planting is done on steep slopes. In plains, the land should be levelled after thorough ploughings. In light rainfall areas, the trees are generally planted during monsoon while in heavy rainfall areas, they are planted at the end of heavy rains. Trees are planted 4.5-6 m apart. Manuring with farmyard manure at the rate of 20-25 kg. per tree together with about $\frac{1}{2}$ kg. ammonium sulphate is done at the time of planting. A fertilizer mixture containing 0.45 kg. each of N, P and K per tree may be applied in the first year planting; in the seventh year and thereafter, the dose may be increased to 0.45 kg. each of N and P and 0.90 kg. K per tree.

Immediately after planting, heavy irrigation is required where trees are grown under irrigation—then light watering follows in 4-5 days. Thereafter, irrigation is given at regular intervals of 8-10 days in hot weather and 12-15 days in cold weather.

To build up strong frame work, young trees are generally pruned. All unwanted branches like water shoots, crossing branches etc. should be removed once or twice a year.

Harvesting—Trees begin to bear fruits from the eighth or tenth year onwards. Fruits are picked during day time. At the time of picking the stem is cut close to the fruit without damaging the rind. Fruits are then graded for size and packed into wooden boxes for marketing.

Uses—Mandarin oranges are used mainly for fresh edible fruits. The essential oil obtained from peel is used in confectionery, toilet products and pharmaceutical preparations. The peel is also used as boiler fuel and for marmalades.

(c) **SOUR ORANGE**—It is also a native of South-eastern Asia. Sour orange is also known as Seville orange. Plant is small tree, 6-9 m in height with blunt spines. Leaves alternate with broad winged petioles. The flowers are exceedingly fragrant. Fruits are large, globose and orange-red in colour, pulp is acidic in taste. Other characters are like those of sweet orange.

In India, this type is not grown commercially. Sour orange is grown in the United States and Spain for ornamental and industrial purposes, it is also used as a stock in grafting.

The oil of neroli, used in perfumery, is obtained from the flower. The leaves are also the source of an essential oil, used in confectionary, cosmetics and perfumery. Fruits are used for marmalade, orangeade and candied orange peel.

Diseases and Insect Pests—

Common diseases are :—(a) Brown rot gummosis caused by *Phytophthora palmivora* and *P. parasitica*—can be controlled by scraping affected bark and applying a wash of zinc-copper lime mixture; applying Bordeaux paint to trunk. dusting holes with mixture of zinc sulphate, copper sulphate and lime (5 : 1 : 4) at the time of planting. (b) *Diplodia* gummosis caused by *Diplodia natalensis*—control like that of (a). (c) Canker caused by *Phytophthora citri*—can be con-

trolled by spraying with 1% Bordeaux mixture; pruning and burning cankered portions. (d) Leaf fall, fruit rot and back canker caused by *Phytophthora palmivora*—can be controlled by pruning dead twigs before monsoon and spraying with Bordeaux mixture. (e) Pink diseases caused by *Corticium salmonicolor* can be controlled by pruning and burning affected branches. (f) Powdery mildew caused by *Oidium tingi*—can be controlled by dusting affected parts with sulphur or spraying with sulphur or Burgundy mixture (5—6—50), (g) Physiological diseases like Mottle leaf due to zinc deficiency, Exanthema due to copper deficiency and Decline due to malnutrition—all these may be controlled by spraying young flush with zinc sulphate lime mixture, applying copper sulphate to soil at 0.21 kg. per tree and applying complete manure regularly every year respectively. (h) Tristeza virus—use of resistant variety and suitable stock-scion combination are the best control measures.

Common insect pests are :—(a) Citrus psylla (*Diaphorina citri*)—can be controlled by spraying with 0.36% nicotine sulphate or 0.02% Endrin @ 4.5-9 litres per tree. (b) Citrus leaf miner (*Phyllocnistis citrella*)—controlled by spraying with 0.5-0.25% DDT or 0.1% BHC or 0.25% Parathion @ 4.5-5 kg. per tree. (c) Citrus white flies (*Aleurocanthis* spp.)—can be controlled by avoiding close planting and spraying with 0.25% BHC or 0.1% HETP or fish oil rosin soap @ 4.5-9 kg. per tree, (d) Fruit sucking moths (*Othreis* spp.)—can be controlled by destroying wild plants on which moths breed, spraying with 0.16% DDT or BHC and covering the individual faints with polythene bags. (e) Orange beetle borer (*Stromatium barbatum*)—can be controlled by burning affected branches and fumigating borer holes with petrol or ED/CT mixture. (f) Citrus green bug (*Rhynchoris humeralis*)—control measure same as for (c).

CHAPTER 6

Beverage-yielding Plants

Beverage is a liquor meant for drinking. Various type of beverages also form some sort of important human food because of their liquid content. Since very early times man was in the habit of finding out palatable drinks or beverages, most of them are plant products and have become of commercial importance. Two types of beverages may be recognised viz. *non-alcoholic* and *alcoholic*.

Non-alcoholic beverages include tea, coffee, cocoa, cola, khat etc. These beverages contain caffeine (an alkaloid) and are used world-wide for their stimulating and refreshing qualities. Of the various beverages, tea which originated in China, is important and used by one-half of the population of the world : next in importance comes coffee, it also originated in regions adjacent to South-western Asia and is now used by one-third of the world's population. Cocoa, a native of tropical America, is also used to-day as both food and drink for many people of the world.

Alcoholic beverages contain alcohol—a poison, which when taken in excess, produces deleterious effects on the human system. Alcoholic beverages are manufactured by the fermentation of sugars present in various fruit juices or sugars produced by the transformation of starch.

6.1 Tea (*Cha, Chaie*): Tea is one of the most important and popular caffeine containing beverage. Tea is obtained from the leaves of the tea plant, the tender leaves are processed into cured products which, when added in boiled water, yield the beverage of the same name. Tea contains 13-18% tannin, 2-5% theine—an alkaloid identical with caffeine and a volatile oil. Volatile oil and alkaloids are readily dissolved in hot water.

Tea has served as principal beverage since the early part of the 5th century, before which it was valued only for its medicinal properties. The word 'tea' has derived from one of the chinese dialects 'te'. China used tea as a popular and delightful drink for the first time and then it was introduced into Japan about A.D. 1000. In India, the use of tea as beverage is known in the works of Albert de Mandelslo (1662) though the actual period was not mentioned in the literature.

Tea plant is botanically known as *Camellia sinensis* (L.) O. Kuntze (Syn. *C. thea* Link.) belonging to the family Ternstroemiaceae. The tea plant in wild condition is an evergreen tree attaining a height of 15-20 m but under cultivation the plant is maintained as a much

branched shrubby bush about 0.6-1.5 m high. Leaves are simple, alternate, exstipulate with lanceolate and leathery lamina having serrated margin and numerous oil glands. Flowers are actinomorphic, hypogynous, bisexual, white or pinkish and fragrant—solitary, axillary at the axil of leaves. Sepals and petals 5, free and imbricate; stamens many, free; carpels 3, united, ovary 3-celled and each cell 2-ovuled. Fruit capsular.

There are two main varieties of *Camellia sinensis* e.g. var. *bohea* and var. *assamica*. The former is the Chinese tea and the latter is the Indian i.e. Assam tea. Chinese variety is a tall plant with soft leaves, it can grow up to an altitude of 1,520 metres while Assam variety is a dwarf bush with leathery leaves and can be grown up to an altitude of 2,432 metres.

Tea is mainly a crop of tropical and hot temperate regions. It is a native of India (Assam) or of China. In India, tea is cultivated largely in Assam, W. Bengal (Darjeeling and Jalpaiguri districts), Kerala and Madras and to a small extent in Tripura, Mysore and Dehra Dun of U. P.

Climate—Tea can be cultivated in the hot temperate and mountainous regions of the tropics. Warm and wet climate favours the growth of tea plant. The average annual rainfall required for tea is between 177-379.5 cm. The best conditions exist when the rain is distributed throughout the year with the heaviest showers during the hottest weather. The suitable temperature requirements lie between 20° and 32°C.

Soil—Tea grows best in well drained, somewhat acidic, deep friable loam or forest land rich in organic matter.

Cultivation—First of all, the area under tea cultivation is to be cleaned by destroying forest growth. The land should be prepared carefully taking in mind three important aspects viz :—(a) protection of land from soil erosion, (b) cultivation primarily for weed suppression and better root development and (c) use of shade trees to protect both the soil and the young plants. Soil erosion can be prevented by employing the correct methods of cultivation, drainage, manuring, green cropping, plucking and pruning.

There are two methods of planting viz. 'square' and 'rectangular' systems. In both the cases, pits measuring 30.4-45.2 cm in depth, 22.8 cm in diameter and 1.2-1.5 m apart in either direction are dug. Before planting, pits are filled with organic matter containing surface soil. When planting is done, plants like *Albizia* spp., *Dalbergia assamica*, *Derris robusta*, *Leucaena glauca*, *Grevillea robusta* etc. are also planted 12.1-15.2 m apart to provide shade to tea bushes.

Tea is normally propagated by seeds but propagation by means of cuttings, budding etc. have been found successful. Seeds are first sown in 'germination' bed, next young seedlings are transferred to 'jungle' or 'basket' nurseries. Then, either 6-18 months old 'basket' seedlings or 1-2 years old 'jungle' seedlings are planted in April-May or

September-October respectively in the pits already dug in the 'square' or 'rectangular' system.

For better growth of the leaves, frequent nitrogenous manuring is essential. Application of heavy amount of compost every year and green manuring are also important. Besides, fertilizer mixtures supplying 27.0 kg. N, 13.5 kg. P_2O_5 and 13.5 kg. K_2O per acre are applied in one or two doses, specially after the pruning of bushes. During rainy season, the garden is hoed and weeded frequently.

Tea bushes are pruned regularly. There are several methods of pruning of which the best one so far employed is as follows :—

1st year after planting—The plant is de-centred by cutting the centre growing stem at 20-30.4 cm from the ground, so as to leave two or more lateral branches which are again cut a little higher up (45.5-50.5 cm). The pruning is done in November and plants are tipped at 75.9 cm from the ground during the following year.

2nd year after planting—Plants are left unpruned and tipped at 84.5-91.2 cm.

3rd year after planting—Plants are pruned flat across at 45.5 cm, removing any strong growing centre shoot leaving lateral branches.

4th and following years—Pruned to leave 1.2 cm of new wood.

Plucking—Tea leaves are plucked by hand or with scissors. The first plucking is usually made when the plants are five years old and is restricted to the terminal bud and two expanded leaves (two leaves and a bud). In North India, plucking begins from April and continues up to December while in the South, plucking continues throughout the year. .

Yield and Grades—The average yield per acre of 'made' tea from seed borne plants is about 226.5-271.8 kg. Vegetatively propagated plants give about 906.0 kg. of tea per acre.

There are generally eight grades of tea, viz :

- | | |
|--|---|
| (a) Broken Orange Pekoe (B.O.P.) | } These three grades are composed of the finer portions of the shoot i.e. the bud, first leaf and the softer part of the stalk. |
| (b) Orange Pekoe (O.P.) | |
| (c) Orange Fannings (O.F.) | |
| (d) Broken Pekoe (B.P.) | } These are coarser grades made mainly from the larger first, second and third leaves and the intervening stalks. |
| (e) Pekoe (P.) | |
| (f) Broken Pekoe Souchong (B.P.S.) | |
| (g) Pekoe Fannings (P.F.) | |
| (h) Dust (D)—It is the smallest grade, consisting merely of grains of tea. | |

Commercial varieties—There are four major commercial varieties of tea e.g. (a) black tea, (b) green tea, (c) brick tea and (d) oolong.

Processing of Tea : (a) BLACK TEA—For the manufacture of black tea, four major operations viz. (1) withering, (2) rolling, (3) fermenting and (4) firing are necessary.

(1) *Withering*—The plucked leaves are taken to withering houses where they are spread out at the rate of 423 kg. leaf to 1 square yard either on slopping wire netting racks or on horizontal hessian cloth 'chung' for 18-24 hours. The main object of withering is to eliminate about half of the water content of the leaves so that they can stand the strain of rolling without breaking up.

(2) *Rolling*—Withered leaves are then taken to rolling rooms where they are subjected to three rolls by machine, each of 30 minutes duration, with 10 minutes between each for unloading, *kutchi* sifting¹ and refilling. This process curls the leaves and buries the cells of the leaves so that their sap is exposed to the action of the oxygen to the air. A low temperature of the room (24-26°C) should be maintained.

(3) *Fermenting*—After rolling and sifting the leaves need to be fermented for a period which depends on weather, temperature and amount of rolling they have undergone. Rolled leaves are spread on a cement floor or some other clean surface of fermenting bed² having 1.2 cm to 2.5 cm thick surface layer for a period varying between 2½ and 4½ hours. Optimum temperature for this process should be low i.e. 24°C or 26.5°C. During this process, tannins present in the leaves are acted on by enzymes—as a result colour of leaves changes from light red to brown.

(4) *Firing*—Fermented leaves are taken from fermenting bed and dried in a current of hot air by 'pressure' type drier machine as quickly as possible. The temperature of the drier should be kept between 60-65.5°C. A sufficiently high inlet temperature (87.5°C—92.5°C) should be maintained to keep the temperature at the top of the machine steady. Time required for firing process varies from 30 to 40 minutes.

The main object of this process is to arrest fermentation and to desiccate leaves slowly to extract the moisture without scorching the tea but at the sametime preserving quality and other characters of tea.

Then the dried tea leaves are passed through sieves of different meshes, thus sorting out 'leaf', 'broken' and 'dust' tea. These are again graded into different grades like B.O.P., O.P., B.P., P. etc. (see page 528). Different grades are then packed carefully in separate plywood tea chests lined with aluminium foil and paper, and thus ready for marketing.

¹ Separation of coarse and fine leaves after rolling.

² It is a bed in which reinforced cement slabs are built in tiers of three with a space of about 5.0 cm between them, they may be made with a slight slope in either direction from the centre; the normal width of a slab is 1.8 m. Aluminium sheet trays may also be used.

(b) **BRICK TEA**—This tea is consumed in Tibet and to some extent in U.S.S.R. Brick tea is manufactured in the following ways :—

(1) *Panning*—Coarse plucked leaves together with twigs are subjected to heat treatment at a temperature of 71-94°C in a large cast iron vessel built into a brick stove for about 10 minutes. In this process, the leaves become a little soft and they turn olive green in colour. No withering is necessary.

(2) *Rolling*—Leaves are then passed to rolling machine in which they are rolled for about half an hour ; in this process the fibre of the leaves being well lacerated and all broken. There is no curling, as the leaves are too coarse.

(3) *Fermentation*—Coarse leaves are placed in a heap upon a mat or upon a cement floor, about 15.2 cm deep (or in case of very dry leaves 0.6-0.9 m deep), covered with a sheet or tarpaulin and left for about five days. The heap generates a considerable amount of heat and after a few days a black fungus begins to grow amongst it—this fungus plays an important role in the fermentation process, typical black colour and flavour of brick tea.

(4) *Drying*—After fermentation is complete, the leaves are dried either in sun or on small brick furnace fired by charcoal. The dried leaves can be kept for long time before moulding into bricks.

(5) *Moulding*—The moulds used in Tibet and China are 1.2 m long and 23.0 cm × 11.3 cm internally with strips in corners. The bulk of leaf, immediately after drying, is rammed as tight as possible into the moulds. Each mould holds material for four bricks of about 1.8 kg. each. After about three days the bricks have settled to allow of the moulds opening. The bricks are then packed in paper and put in the sun.

(c) **GREEN TEA**—This type of tea is mainly produced in China and Japan. The main feature in the manufacture of green tea, as distinguished from black tea, is that the green tea does not require artificial withering and fermenting processes. Instead natural withering or wilting is done which retain the greenness of the leaves. Following operations are followed in the manufacture of green tea :—

(1) *Panning*—This process is done in the same way, as described for brick tea.

(2) *Steaming and Rolling*—In this process, leaves are first heat treated at about 120°C either by pan-firing or by steaming. As soon as the leaves have become soft enough, they are rolled by hand on a bamboo mat.

(3) *Drying*—Next, rolled leaves are taken to brick furnace where they are dried upon trays over charcoal fires until they are perfectly crisp.

(d) **OOLONG TEA**—This is an intermediate type between black and green teas. Oolong tea is partially fermented and has the colour of the black tea and the flavour of the green tea. Oolong tea is mainly produced in Formosa.

Diseases and Insect Pests—

Common diseases are :—(a) Red rust and algal red spot caused by *Cephaeleuros parasiticus*—can be controlled by proper manuring and spraying with Bordeaux mixture during monsoon or lime-sulphur during cold weather. (b) Blister blight caused by *Exobasidium*—can be controlled by spraying with Perenox, Cuprokylt or Blitox or dust with 4% Cuprosana every week or ten days. (c) Brown blight caused by *Colletotrichum camelliae*—can be controlled by pruning all dead and discoloured wood, also by spraying with Bordeaux mixture. (d) Bird's eye spot caused by *Cercospora theae*—control by spraying with 0.5% Bordeaux mixture. (e) Copper blight caused by *Guignardia camelliae* and *Laestadia theae*—can be controlled by burning affected leaves, spraying with Bordeaux mixture, spraying bushes with soda solution and first flush with Bordeaux mixture after pruning. (f) Dieback caused by *Nectria cinnabarina*—can be controlled by pruning diseased bushes back to good wood and spraying with Bordeaux mixture. (g) Stump rot caused by *Irpex destruens*—can be controlled by applying coal tar to pruned cuts. (h) Root rot caused by *Botryodiplodia theobromae*—can be controlled by treating soil with lime @ '84 kg. per bush during the early stage of disease, also by burning all infected materials.

Common insect pests are :—(a) Red spider (*Tetranychus bioculatus*)—can be controlled by spraying with lime sulphur (1 : 2 : 16) or 0.24% Aramite @ 270—360 litres per acre. (b) Tea mosquito (*Helopeltis* spp.)—can be controlled by destroying bugs in kerosenised water and spraying bushes with 0.1% DDT @ 270—360 litres per acre. (c) Tea looper (*Buzura suppressaria*)—can be controlled by spraying with 0.16% DDT @ 270—360 litres per acre. (d) Tea red slugs (*Heterusia* spp.)—control measure is same as under (c). (e) Bagworm (*Clania crameri*)—control is same as under (c). (f) Termites (*Microtermes* spp.)—can be controlled by adding 5% Aldrin or Dieldrin dust in the soil @ 9 kg. per acre.

6.2 Coffee (Kafi) : From the commercial point of view, coffee stands well amongst the popular and important beverages. Coffee is grown mainly for seeds. The seeds are roasted and ground into powder, which when soaked in boiling water yields a fragrant and stimulating beverage. The roasted coffee seeds contain 0.75-1.5% *caffeine*—the stimulating agent and a volatile oil—*caffeol* which is responsible for the flavour and aroma.

The chief coffee producing regions of the world are Arabia, West Indies, Java, Brazil, Colombia, Venezuela, Salvador, Haiti, Indonesia, West Coast of Africa, Ceylon etc. In India, coffee is grown largely in South India on the foot hills of western Ghats in Mysore and the sub-regions of eastern Ghats in Tamil Nadu and Kerala, it is also produced in Andhra Pradesh.

The coffee plant is a native of Abyssinia from where it was introduced in Arabia about 500 years ago. Gradually it was introduced in tropics and reached Ceylon, Java, West Indies and Brazil. In India, the cultivation of this plant was undertaken since the early part of the 19th century.

Coffee plant belongs to the genus *Coffea* under the family Rubiaceae. The genus *Coffea* includes several species of which only

three species e.g. *C. arabica* L., *C. liberica* Hiren and *C. robusta* Linden are in cultivation and commercially important. Of the three species, *Coffea arabica* is the better one and is the source of arabian coffee which supplies about 20% of the world consumption; it is a native of Abyssinia. In India it is grown in South India and Travancore. *C. liberica* is the source of liberian coffee—a native of West Coast of Africa. In India it is grown in Mysore and Travancore. *C. robusta* is the source of congo coffee—a native of Congo. In India it is cultivated in Madras, Mysore and Travancore. There is another variety known as highland coffee of Sierra Leone obtained from *C. stenophylla* G. Don, but this species is not commercially important.

Coffea arabica is a beautiful evergreen shrub or small tree attaining a height of 4.5-9.1 m. Leaves are opposite, stipulate (inter- or intrapetiolar), shining. Flowers axillary in fascicles, white, fragrant, star-like, bisexual, epigynous. Sepals in a short tube, 4-toothed. Petals 4-5, connate in a funnel-shaped corolla, lobes spreading, contorted. Stamens 4-5, sessile. Carpels connate in 2-celled inferior ovary. Fruits are small fleshy berries changing in colour from greenish yellow, red to crimson. Seeds planoconvex, concave or grooved on septal side, greenish-grey in colour, covered with a thin membrane (a silver skin) and enclosed in a dry husk-like parchment.

Climate—Humid climate having a well distributed rainfall of about 202.4 cm or more and a temperature ranging from 12.5°-32.2°C is the most suitable for coffee cultivation. For the ripening of the bearing wood, a spell of dry climate in December and January is necessary.

Soil—Coffee grows well on deep, rich and well-drained forest loam having a gentle slope.

Cultivation—Coffee can be cultivated from sea level to an altitude of 1,529 metre. First of all the land should be cleared by cutting all unwanted plants. Generally steep slopes having contour drains are terraced. Along the contours, pits 45.6 cm × 45.6 cm and 46.6 or 60.8 cm deep are dug during January to April; the distance between successive rows and adjacent pits in rows being 1.5-1.8 m. At the time of planting, pits are filled up with soil mixed with farmyard and green manures. In India, shade trees are planted one year before the planting of coffee plants at suitable distances to provide protection against too much heat and rains, and also against soil erosion.

Coffee plants are grown from seedlings which are raised from seeds in nursery beds. Healthy seeds are sown in January—March, 5.0-7.5 cm apart in well manured raised nursery beds (15.2 cm high, 91.2 cm wide and 60.9-1 m long) surrounded by channels. The seeds are then covered with leaf mould and watered twice a day or once daily. Germination takes place within 6-8 weeks. During March—May, when seedlings attain a height of 50 cm then are transplanted 30.4 cm apart in another raised and shaded nursery bed or

individually in suitable sized baskets filled up with farmyard manured forest soil. In this stage seedlings are regularly watered, weeded and sprayed with Bordeaux mixture. When the seedlings become one year old they are transplanted in the pits of the permanent land during rainy season from June to September. The young plants are generally tied to thin stakes for support.

Every year, manuring of the land with cattle manure or compost at the rate of 5-10 tonnes per acre is essential. Besides, a fertilizer mixture containing 13.5-18.0 kg. N, 18.0-27.0 kg. P_2O_5 , 36.0 kg. K_2O per acre should be applied annually in two doses, one before the monsoon and the other after monsoon. Weeding and deep digging operations are necessary in the first year after planting. Subsequently two weedings, one in February-March and another in September-November are given. Main stem of the plants is tipped twice, once when they attain a height of 0.62 m and the other one when they are about 1.5 m. The berries *i.e.* fruits begin to develop on the nodes of one year old branches. These one year old fruit bearing branches are pruned after the harvest. Generally pruning is followed in the form of a single stem umbrella—in this method bushes tend to develop a dense upper canopy of crop bearing branches.

Harvesting and Yield—Coffee plant begins to bear fruits for yield in the third or fourth year and continues for about 50 years. The fruits are ripened within 8-9 months. Fruits of *C. arabica* are harvested during October–December while of *C. robusta* in January–March. Mature fruits are usually picked by hand, in some places they are stripped off or allowed to fall to the ground.

The average yield of *C. arabica* is about 226.5-271.8 kg. of 'clean' coffee per acre while *C. robusta* yields nearly double the amount of *arabica*.

Processing—There are two methods of the processing of coffee for the market *e.g.* the *dry method* and the *wet method*. 'Cherry' or 'Native' coffee is obtained by dry method while 'Plantation' or 'Parchment' coffee results from the wet method.

In 'dry' method, the fruits *i.e.* berries are spread on the floor exposing to the sun, precaution being taken to protect them from rain. Then the berries are stirred constantly so that they are dried uniformly. Next, the dried skin and pulp are cleaned off by peeling machines and the parchment is removed either by pounding in a mortar or by any other mechanical means. The seeds or 'coffee beans' are then sorted by sieving into different grades, of which large round beans from single seeded fruits forming top grade and packed in bags for transport.

In 'wet' method, the berries are processed through a pulping machine, as a result the skin and part of the pulp are removed—they are then placed in vats for fermenting. In this process rest of the pulp ferments and which are washed off in water; then they are finally

dried in the sun or by artificial heat. After drying, the brittle parchment and the skin are peeled off by machines.

The beans obtained by the above mentioned processes are roasted. During this process, aroma, flavour and colour develop. Roasted beans are ground before coffee is sold to the market.

The broken, deformed and dark coloured beans constitute the lowest grade known as 'triage'.

Diseases and Insect Pests—

Common diseases are :—(a) Rust or leaf diseases caused by *Hemileia vastatrix*—it can be controlled by growing resistant variety and spraying Bordeaux mixture. (b) Black rot caused by *Pellicularia koleroga*—can be controlled by spraying Bordeaux mixture. (c) Dieback caused by *Colletotrichum coffeanum*—it can be controlled by the application of heavy manure at the time of maturation and also by providing good drainage. (d) Nursery damping off and collar rot caused by *Pellicularia filamentosa* (Syn : *Rhizoctonia solani*)—can be controlled by reducing nursery shade and watering ; also by drenching seed bed with Perenox (56·8 ml in 5·0 litres per 24 sq. ft.) & Fermate (28·4 ml in 5·0 litres etc.). (e) Brown eye spot caused by *Cercospora coffeicola*—control measure by reducing shade in nursery and spraying the lower surface of leaves every fortnight with 1% Bordeaux mixture. (f) Physiological diseases like black bean—no definite control measure is yet known.

Common insect pests are :—(a) White borer (*Xylotrechus quadripes*)—can be controlled by removing and destroying eggs, wood and infested parts ; by spraying with 0·25% DDT @ 9·0—13·5 litres per plant or scrubbing the stems with 1% BHC suspension. (b) Scale insects (*Lecanium* and *Saissetia* spp.)—control by pruning infested shoots and spraying with fish oil rosin or 0·02% Parathion or 0·1% HEP @ 9·0—19·5 litres per plant. (c) Red borer (*Zenzora coffeae*)—can be controlled by removing affected branches.

6.3 Cocoa or Cacao (Koko) : In India cocoa is a crop of minor importance although it is widely cultivated in western countries for its palatable drink. It is not only used as beverage but also as food in the manufacture of chocolates and cocoa powder. The cocoa butter obtained from seeds is used in cosmetics and perfumery.

Cocoa is a native of tropical America. In India, it was introduced about 150 years ago and its cultivation in this country is restricted to the foot hills of Nilgiris and in some parts of Kerala. Generally two varieties of cocoa viz. *Forastero* and *Criollo* are cultivated. *Forastero* variety yields coarse product but contributes 95% of the world supply. *Criollo* yields fine product—it is commonly cultivated in the Nilgiris.

Cocoa is obtained from the seeds of the plant *Theobroma cacao* L. belonging to the family Sterculiaceae. Plant is a branched small tree attaining a height up to 7·6 m. Leaves simple, stipulate, alternate—lamina shining, ovate and often 0·3 m in length. Flowers bisexual, regular, hypogynous developing in clusters from the old wood. Sepals 5, free, valvate. Petals 5, free, imbricate. Fruits are pod-like capsules, 15·2-23·2 cm long and 7·5-10·0 cm thick with tapering ends. Each fruit contains mucilaginous pulp and several seeds numbering up to 40 ; the colour of ripe fruits often changes from green to reddish

purple or yellow. Seeds are pale to deep purple in colour and with fleshy endosperm.

Climate—Cocoa is a tropical crop and requires a warm and moist climate. Drought and wind are injurious to cocoa. It is grown in areas with rainfall up to 506-759 cm annually. The temperature requirements range from 32.5° to 65°C.

Soil—A deep well-drained alluvial soil rich in organic matter and capable of retaining abundant moisture is the best for cocoa planting. It can be grown also on loamy soil.

Cultivation—Selected land is dug and pits measuring 0.6m × 0.6m × 0.6m and 4.5m apart in either direction are made. Shade trees of leguminous type may be planted while other unwanted plants are removed.

The crop is raised from seeds or transplanted seedlings. One year old seedlings from nursery beds are transplanted in pits with the individual plants in rows at 1.2 or 1.5 m intervals at the beginning of south-west monsoon; they are provided with thatched shade in the beginning and later by tree shade. The soil is frequently weeded and hoed.

Harvesting and Yield—The plant begins to bear fruits in the third year of planting but full bearing stage is reached in 7-10 years. The fruit generally ripens in four months. The ripe fruits are picked twice a year, the first one in April-May and the second in November-December.

The average yield of dry seeds per acre varies from 180—226.5 kg.

Curing—Seeds or 'cocoa beans' are carefully taken out from the harvested fruits or pods by cutting them with the help of a sharp knife. The seeds are then fermented in specially made sweating boxes or 'troughs', rarely they are dried in the sun. The seeds are constantly stirred during fermentation. This process lasts for about a week and during this fermentation process, the seeds become brownish-red in colour, lose their bitter taste and develop aroma due to deposition of characteristic chemical compound known as *theobromine*. When fermentation is over, seeds are washed, dried in the sun and polished either by machines or the feet of the local people to remove any dry pulp.

From these cured seeds or beans commercial cocoa and chocolate are prepared. The seeds are roasted at a temperature of 131.5°C-140°C in iron drums. Now flavour of the seeds develops. Next roasted beans are passed for grinding between corrugated rollers which break the brittle shells into small fragments. Small fragments of shells are removed in a winnowing machine. Seeds are then ground to oily paste from which cocoa, chocolate etc. are made.

Cocoa is prepared by removing about $\frac{3}{4}$ rd fatty oil of the ground seeds in hydraulic process and powdering the residue. Oily paste when cooled and hardened, become the 'raw' or bitter chocolate of commerce. From the bitter chocolate, sweet chocolate, is made by

adding sugar and other aromatic materials. The fatty oil, removed from the seeds, forms the 'cocoa butter' used in perfumery and cosmetics.

Diseases and Insect Pests—

Common diseases are : (1) Black pod caused by *Phytophthora palmivora* is the most widespread disease, which in many cases destroys up to 40% of the potential crop—it can be controlled by spraying with Bordeaux mixture. Black pod disease causes decay of fruit, leaf and shoot. (2) Anthracnose disease caused by *Glomerella cingulata* induces fruit and leaf spots, it causes chronic leaf-fall or bare tip—can be controlled by copper sprays. (3) Pod rot caused by *Monilia royeri*. (4) Witches'-broom caused by *Marasmius perniciosus*. (5) Root rot and bark splitting caused by *Rosellinia* sp. and (6) Swollen shoot (a virus disease)—the remedy being to cut out and burn affected trees.

Common insect pest is Mealy bug (*Pseudococcus citri*)—can be controlled by pruning infested shoots and spraying with fish oil rosin or 0.02% Parathion or 0.1% HETP @ 9.0—13.5 litres per tree.

Some Beverage yielding plants of minor importance :

(a) *Cassine* (*Ilex vomitoria*, Aquifoliaceae) : A beverage called *yaupon* is prepared from the dried leaves and shoots of the plant, which is a small tree or shrub. It grows in North America, specially along the coast from Virginia to Mexico. The beverage contains caffeine and tannins. It is prepared in the same way as tea. Now-a-days, cassine is added as a stimulant to other drinks or beverages.

(b) *Cola* (*Cola nitida*, Sterculiaceae) : The seeds of this plant are ground, added to water and boiled for the preparation of a drink. *C. nitida* is native of tropical West Africa, cultivated mainly in Ghana and Nigeria. It has also been introduced in some parts of tropical America as well as in India. The chemical composition of seeds include caffeine (2%), theobromine (trace) and colanin—a glucoside.

(c) *Guarana* (*Paullinia cupana*, Sapindaceae) : is a beverage used chiefly in the Mato Grosso region of Brazil. The drink is prepared from the seeds of *P. cupana*, which is a small shrub in the cultivated form. The seeds are dried, ground, made into a paste with cassava flour, formed into pieces resembling sausage and dried in smoke. For preparation of the drink, the dried, hard pieces are grated and mixed with either hot or cold water. Guarana contains 4-6% caffeine and is stronger than coffee.

(d) *Mate*, *Yerba mate* or *Paraguay Tea* is prepared from the *Ilex paraguayensis* (Aquifoliaceae) : The plant is a small tree or shrub, native to the mountainous regions of Northern Argentina, Paraguay, Uruguay and Southern Brazil. Every second or third year the young shoots are harvested, dried over a fire, beaten with sticks to separate the leaves. The leaves are then dried in special ovens, crushed and made ready for use as beverage. The leaves contain about 1% caffeine. Mate is the most popular stimulant beverage of South America and is prepared like tea. It has a slightly bitter taste, slight aroma and a light green colour.

CHAPTER 7

Drug-yielding or Medicinal Plants

Man is using lots of plants as drugs in curing diseases or to relieve physical sufferings since the earliest times. During 5,000—4,000 B.C. many drug plants were in use in China. The use of various plants as drugs can also be obtained from the earliest literature written in Sanskrit, Hebrew, Greek etc.

Practically all plants are medicinal, but the drug plants which are in cultivation and largely used in curing diseases are recognised as drug-yielding or medicinally important plants.

This Branch of Botany (i.e. Economic Botany) which mainly deals with the drug plants themselves, is now-a-days termed as *pharmacognosy*. Pharmacognosy is concerned “with the history, commerce, collection, selection, identification and preservation of crude drugs and raw materials.” The study of the action of drugs comes under *pharmacology*. Although several thousand plants have been used for medicinal purposes by aborigines and native people, still a considerable number have been standardised¹ as official drugs—the active principles of which are referred to in the Pharmacopoeias e.g. British Pharmacopoeia (B. P.), Indian Pharmacopoeia (I. P.), Homeopathic Pharmacopoeia (H. P.), United States Pharmacopoeia (U. S. P.), National Formulary (N. F.), etc.

The medicinal value of drug plants is mainly due to the presence of some chemical substance or substances in the tissues. These chemical substances are mainly C, H, O and N containing alkaloids which, if introduced into the human body, produce a definite physiological action, i. e. either beneficial effects in the treatment of diseases or harmful effects causing even death.

Gums, resins, essential oils, glucosides, tannins etc. are also used in drugs.

In India, a large number of drug plants grow in a state of nature and some are also cultivated under various climatic, meteorological and topographical conditions. Those cultivated plants possess properties and cause actions similar to the imported and often expensive remedies and form excellent substitutes.

Drug-yielding plants are generally classified on the basis of the nature of chemical substances or their therapeutic value. But for convenience, they are also classified on other characteristic features.

¹ As a result of the Drug Act of 1906

7.1 Ipecac : Ipecac or ipecacuanha is an *emetine-yielding* plant. The botanical name of this plant is *Cephaelis ipecacuanha* (Brot.) A. Rich (Syn. *Psychotria ipecacuanha* Stokes, *Uragoga ipecacuanha* Boil) belonging to the family Rubiaceae. This plant is an exotic one and a native of Brazil.

In India, ipecac plant was first introduced into the then Royal (now Indian) Botanic Garden, Calcutta. Now it is growing successfully for a period of over 90 years in the lower ranges and foothills of Terai and Duars of Darjeeling and Jalpaiguri districts specially at Mungpoo, in the Nilgiri hills near Kallar in Madras and to some extent in Bombay State. It is also cultivated at the Rungbee Cinchona plantation in Sikkim.

Ipecac plant is a straggling evergreen perennial herb with decumbent stem with root much branched, moniliform or beaded. Branches developing from the underground base of the stem often with hairy roots. Stem green, more or less succulent. Leaves opposite, with interpetiolar stipules, ovate or obovate, elliptic, 5.10 cm × 3.6 cm., dark green, glabrous and shining above. Flowers dimorphic, bisexual, epigynous; crowded in small cymose head, white, odourless. Corolla funnel-shaped. Sometimes florets are heterostylous. Ovary inferior, round; stigma short. Fruits, berries in a cluster, round or oval, dark purple or blackish. Seeds creamy-white, flat, more or less plano-convex.

Climate—A very moist but frost free atmosphere almost similar to that of “rain forest type” is suitable for ipecac cultivation. The annual rainfall should be between 254.0 cm and 508.0 cm during monsoon and the later part of winter and spring. The minimum and maximum temperatures should be ranging from 10°C to 20°C respectively.

Soil—Ipecac grows well in a well-drained, sandy loam soil rich in humus.

Cultivation—Ipecac is cultivated in a levelled and spacious land, if possible in a virgin forest land and between an elevation of about 304.5 m and 609.5 m. In case of flat land, it is slightly levelled to form terraces of 4.0 m wide.

Ipecac plant may be propagated from seeds, root and stem cuttings, layerings and matured leaf cuttings.

Seed Propagation—The seeds are first sown in well-prepared raised nursery beds. The nursery is divided into two plots, locally called *kamras* (in Darjeeling district), of 1.8m × 1.8m; a slanting *machan* is built (1.6 m high at one end and 0.75 m at the other end) over the bed and the bed is protected along the sides with pieces of timber. The bed is then raked over and 4-6 baskets of leaf soil and one basket of sand are added to each *kamra* and dug in. Then seed bed is levelled off and thoroughly watered; lastly a layer of riddled soil is placed 2.5 cm thick on the top. The bed is now ready for seed sowing. About 85-141.5 gms of seeds are

sown in a *kamra* of 36 sq. ft. from January to March either broadcast or in drill. Germination takes place within 4-5 months. During this stage watering and weeding are very essential. After germination, seedlings are transplanted 5.0 cm apart to another i.e. 2nd nursery—built and prepared in the same way but with double the amount of leaf soil and sand, and this is done during July-August. In the following year during March-April, seedlings are again transplanted to another i.e. 3rd nursery with a 13.0 cm spacing both ways, where they will remain till uprooted. In this stage, seedlings are watered carefully and given a top dressing annually or biennially with well-rotted cow manure and sand. The usual weeding and watering are continued till the time of harvesting. Ipecac is mainly a shade-loving plant, hence protection against exposure to sunlight should be maintained by planting leguminous shade-trees alongside the bed.

Harvesting, Yield and Storage—Plants are uprooted after three or four years from the time of sowing the seed. Seeds are collected at the end of the first year of 13.0 × 13.0 cm planting. During the second and third years more seeds and layers are collected. At the end of the third year or at the beginning of the fourth year, the layers are removed, the radix is uprooted and all the cuttings are taken out. Radix is then thoroughly washed and dried. The yield of dry radix from a *kamra* of 1.8 × 1.8 m varies from '63—'84 kg. The prepared ipecac should be kept in airtight container and stored in a cool room.

Vegetative Propagation—Ipecac plant may be propagated vegetatively from cuttings in the following way :—

The cuttings from root, stem and leaves are placed in a sand containing pans 7.6 cm deep. They are kept constantly moist and under cover for protection from the direct sunrays and a drip. Under favourable conditions, callus develop from cuttings within two to three weeks. After this a mass of fibrous roots grow out from the callus, then young shoots appear above the ground. The young plants are then potted off when they are about 2.5-3.7 cm in height into pans, not less than 13.0 cm deep. Plants are finally planted into beds when they are about 10.0-15.2 cm high.

Alkaloids of the Ipecac Plant—Alkaloids obtained from the powdered bark of the root of ipecac plant are classified into two sub-groups such as, (1) *Non phenolic sub group* which contains emetine ($C_{20}H_{40}O_4N_2$), O-methylpsychotrine ($C_{29}H_{38}O_4N_2$), emetamine ($C_{29}H_{38}O_4N_2$) and (2) *Phenolic sub group* containing cephaeline ($C_{29}H_{38}O_4N_2$) and psychotrine ($C_{28}H_{38}O_4N_2$). Alkaloids in the form of white powder are obtained by drying the powdered bark of the root with a little milk of lime and exhausting the mixture with boiling chloroform, ether or petroleum benzene. The total alkaloid content of Indian roots is 1.98% of which 1.39% emetine : whereas the Brazilian roots contain 2.2-7% of total alkaloids with 1.35% emetine.

Uses—Ipecacuanha powder is used largely in the treatment of dysentery. In diarrhoea and in some forms of dyspepsia, it acts bene-

ficially. As an expectorant it is in common use in chronic bronchitis, asthma, phthisis etc. It is also useful in uterine haemorrhages and in menorrhagia.

Diseases and Insect Pests—Common diseases are due to the presence of some soil fungi in soil e.g. *Fusarium solani*, *Rhizoctonium hisroglypticum*—they can be controlled by the development of resistant varieties, and also by treating seeds with different fungicides.

Common insect pest is red ant (*Oecophylla amarogdina*)—can be controlled by burning and destroying the nests or spraying 0.25% BHC on the nests.

7.2 Rauvolfia (*Sarpagandha*, *Chandra*, *Chotachand* etc.): The genus *Rauvolfia* (Syn. *Rauwolfia*) belongs to the family Apocynaceae. It contains several species e.g., *Rauvolfia densiflora* B. & H., *R. perakensis* King & Gamble, *R. canescens* L. and *R. serpentina* Benth. Of these species, *Rauvolfia serpentina* is the most important one regarding its medicinal importance and was known in India from very ancient times while *R. canescens*, though found growing wild in various parts of East India, is an exotic plant introduced from West Indies.

Rauvolfia serpentina is found to grow in India along the lower elevations of the Himalayas up to an altitude of 1200 m, extending to Sikkim, Khasia hills and Assam, in the western and eastern areas of Peninsular India, Bihar, Dehra Dun, W. Bengal and Andaman Islands.

Rauvolfia serpentina, is a small perennial glabrous shrub, 0.4-0.6 m high—sometimes the plant is branched. Leaves whorled, simple, exstipulate, tapering at the ends, upper surface shining and smooth while lower surface is pale green. Flowers are bisexual, regular and hypogynous, white or pinkish in colour, produced in cymes. Calyx 5-partite. Corolla salver-shaped with 5 petals. Stamens included, epipetalous, anthers small, acute. Disk large, cupular or annular. Carpels 2, connate, style filiform. Fruit drupe-like, 1-seeded.

Climate—It can grow in all climatic conditions nearly all over India. In natural condition, it is found in plains up to an elevation of 1,000 metres. High rainfall (155.0-506.0 cm or more per annum) induces good growth of the plant.

Soil—*R. serpentina* can grow best in neutral or slightly acidic soil composed of sandy loam and leaf-mould having proper drainage.

Cultivation—*R. serpentina* has been successfully cultivated in many places of India both in the plains of West Bengal, U.P., Orissa as well as in the hills of Assam, Darjeeling (Mungpoo, Rongo, Jaldhaka) Jammu and Kashmir, Nepal, Bhutan, western and eastern Ghats etc. Areas having favourable climatic and edaphic conditions are the best for successful large-scale cultivation.

There is no hard and fast rules or special methods for the cultivation as the plant is "to adapt to its local environmental conditions". *Rauvolfia serpentina* is propagated by seeds, root cuttings and stem cuttings. Of these, propagation by root cuttings gives 75% yields while stem cuttings yield 50%. Direct sowing of seeds by broadcast

gives better growth, larger quantity of root and higher alkaloids. The cultivated land is first ploughed a few times, than harrowed and laddered. Generally, leaf soil and farmyard manure with pinches of bonemeal are applied to the soil before planting. Cleaned and washed seeds are sown in July-August in seed beds and then transplanted in the prepared land during August-September. The seeds may also be sown before monsoon after normal preparation of the land. During dry season irrigation is necessary for the increased growth of roots and in the production of seeds. Partial shades are preferable to direct exposure to sunlight.

Harvesting and Storage of Roots—Roots with their intact bark of 3-4 years old plant are generally harvested during winter, since the alkaloid content of the root increases during winter than during other seasons. Of the roots harvested, about 50% are pieces of thick tap root, 25% are branch and the rest 25% are hairy roots. The harvested roots are washed thoroughly and properly dried under the sun. Dried roots are powdered, then strained through a piece of muslin and finally stored up in various airtight containers.

Yield—The average yield per year of air-dried roots after the third year varies from 800 to 1,500 kg. per acre.

Uses—The uses of *Rauvolfia serpentina* are various. It is a tonic and febrifuge. Javanese people use it as an anthalmentic. The juice of leaves is used for removal of opacities of the cornea of the eyes. The roots are used mainly in the treatment of mental disorders, hypertension etc. The alkaloid *reserpine* is used in lowering high blood pressure. In case of insomnia and nervous breakdown, it is given as a sedative. The decoction of root is used to increase uterine contractions in labours.

Alkaloids of the Rauvolfia Plant—About 80 alkaloids are found in different species of *Rauvolfia* and about 20 alkaloids have been isolated from *R. serpentina*. The important alkaloids are reserpine, reserpinine, ajmaline, sarpajmaline, ajmalicine and serpentine. Alkaloids 3-epi-yohimbine, riseinnamine, rouwolfinine ($C_{18}H_{24}O_4N_2$) etc. have also been isolated from both *R. canescens* and *R. serpentina* (Chopra and Handa, 1961).

7.3 Cinchona (Sinkona, Quinine): The well known and the most important drug 'quinine' is obtained from the hard and thick barks of *Cinchona* plant.

Cinchona plant belongs to the family Rubiaceae and is a native of the Andes, South America. It was first introduced in Java and India by the Dutch and the English respectively. The main centre of *Cinchona* culture practically started in Java. The drug obtained from *Cinchona* was first used by an English lady, the Countess of Cinchon—the wife of the Viceroy of Peru in the year 1638. In India, the plant was brought from Java by the efforts of T. Anderson. He planted it in the Royal (now Indian) Botanic Garden, Calcutta.

Then gradually the plant was introduced to the mountainous regions of Bengal for large scale cultivation.

There are several species of *Cinchona* of which only four species, e.g., *Cinchona calisaya* Wedd., *C. ledgeriana* Moens, *C. succirubra* Pav. ex Klotzsch and *C. officinalis* Linn. are cultivated in India for the commercial cinchona bark from which the drug 'quinine' is manufactured.

Cinchona calisaya is found to grow in the Moyal valley in Nilgiris and Sikkim at altitudes ranging from 457.0 to 914.0 m. The plant is a robust and large tree. Leaves simple, stipulate, glabrous, thick, oblong-lanceolate or oblong-obovate, shining above. Flowers pale flesh-coloured in cymes. Fruit ovoid-oblong capsule, 8-17 mm long.

The bark is thick, white, smooth and distinctly fissured. The bark is known as Peruvian, calisaya or yellow bark of commerce.

C. ledgeriana is grown in hilly tracts of W. Bengal (at altitudes of 914.0—1,828.5 m, the Khasia and Jaintia hills (1,524 m) and in Tinnevely district in S. India. The plant is a small, weak and straggling tree attaining a height of 6 m. Leaves are thick, glabrous and elliptic. Flowers are yellow. Fruits are ovoid-lanceolate capsule, 8-13 mm long. Bark obtained from this plant is known as Ledger bark of commerce.

C. succirubra is grown at varying altitudes from 609 to 1,828.5 m in Sikkim, S. India and in the Satpura range and Madhya Pradesh. The plant is a tall erect tree, reaching a height up to 15 m. Leaves are thin, broad, large, elliptical. Flowers are rosy in colour. Fruits are oblong capsule, 25-32 mm long.

Bark is brown in colour with a few white markings and transversely fissured; commercially the bark is known as Red bark.

C. officinalis is found to grow in Ootacamund, S. India. The plant is a slender tree up to 9 m in height. Leaves are small, glabrous, ovate-lanceolate, shining above. Flowers are rose-coloured. Fruits are ovoid-oblong capsule, 17-20 mm long.

The bark is brown outside and yellow within, rough in texture with black and white markings, transversely cracked. Commercially this bark is known as Crown or Loxa bark.

Climate—*Cinchona* grows well in tropical climate at altitudes of 914 to 1,828.5 m. A high atmospheric humidity and the evenly distributed rainfall throughout the year ranging from 253 to 379 cm per annum favour the growth of the plant. The average temperature requirement ranges from 15.5 to 24°C.

Soil—*Cinchona* plant thrives well in a porous, well-drained virgin forest soil rich in organic matters. Acidic soil having pH ranging between 4.2-5.6 is also suitable for cinchona. Water logged condition of the soil is very injurious to the plant.

Cultivation—Plants may be propagated from seeds or vegetatively from cuttings and layerings. But in India seed propagation is more

effective and common practice than vegetative propagation. Normally hill-slopes protected from the blasts of wind are selected for the cultivation. The site should be cleared by removing forest vegetation and then dug about 0.5 m deep. Next the virgin forest soil is well manured with leaf mould and sand is sprinkled over it. Some portions of the forest should be kept as it is, so that they may serve as wind screens. Seeds are then sown broadcast in well-prepared sloping beds (3.5 m × 1.2 m), covered by a thatch roof. Immediately after sowing heavy watering is essential. Within three to six weeks, seeds germinate. When seedlings attain a height of 2.5 cm and are provided with 2-3 pairs of leaves, then they are transplanted in well-prepared nursery beds in lines, with 5 cm spacing in both ways. At first, seedlings are provided with shades, but shades are gradually removed as soon as they increase in size. Seedlings, when they become 14-18 months old and attain a height of 0.5-0.6 m, are finally transplanted in the pits of well-prepared field with a spacing of 1.2 × 1.2 m—this is done before monsoon but generally in moist and cloudy weather. The young plants in the field are shaded with shade trees. Shade trees are generally planted 6 m apart.

Harvesting, Yield and Processing—The bark is harvested from the trees when they are about 10-12 years old. The branches are removed and the trunk is cut down above the ground, leaving behind a stump of about 1.5 m. Sometimes the stump along with the root is also dug out. Then the bark is removed from these with a knife. The harvested bark is then dried in artificial chamber at a temperature below 75°C. The dried bark is then packed in gunny bags and then stored up in a room.

The average yield of dry bark per annum varies from 11,000 to 12,000 metric tonnes.

The dried bark is first "treated with soda lime, extracted with alcohol and evaporated off. The residual solution is taken up in dilute acid, filtered through cotton and the precipitates are washed with dilute acid several times. The filtrate is then made alkaline and extracted with chloroform. The chloroform extract is evaporated and the residue weighed."

Alkaloids and Uses—The main alkaloid of the bark is *quinine* ($C_{20}H_{24}O_2N_2$), it is white and very bitter—mainly used in the treatment of malarial fevers. Quinine is also used as a tonic and antiseptic and in the treatment of fevers. Other important alkaloids of the bark are cinchonidine, cinchonine, quinidine, quinicine, cinchotine, quinamine, hydroquinidine etc. ; all of these are used in medicine as standard mixture.

Diseases and Insect Pests—*Common diseases are* :—(1) Stem blight caused by *Sporotrichium* and *Verticillium* spp. (2) Seedling blight caused by *Phytophthora palmivora* and (3) Root rot caused by *Sclerotium rolfsii*—all these may be controlled by continuous changing of nursery site, disinfecting soil and through early transplanting. Of the *insect pests*, grubs of cockchafer beetles (*Holotrichia repetita*, *Rhizotrogus* spp.) cause serious damage to seedlings of cinchona ; sometimes leaf bugs (*Disphinctus humeralis*) are also found on young leaves—all

these may be controlled by removing adults through hand picking and by irrigating seed beds with water mixed with crude oil emulsion.

7.4 A Few Important Durgs and Drug-yielding Plants

(a) **ABROMINE**—It is an alkaloid obtained from the roots and root bark of the plant *Abroma augusta* L. f. (Sterculiaceae). Abromine is used in dysmenorrhoea. The plant is a shrub or small tree ; it is cultivated in Assam, Khasia hills and U.P.

(b) **ACONITINE**—This alkaloid (aconitine) is obtained from the tuberous roots of *Aconitum napellus* Wall. (Ranunculaceae). It is cultivated in temperate regions of India (e.g. Himalayas) both as an ornamental and as a drug plant. Aconitine i. e. aconite is used externally for rheumatism and neuralgia and internally to relieve fever and pain.

(c) **ALOE**—From the leaves of several species of *Aloe* (Liliaceae) glucoside containing resinous juice is obtained. Aloes are used as purgatives. This plant with succulent leaves and showy flowers is cultivated in many parts of tropical countries.

(d) **ATROPINE**—It is obtained from the dried leaves of *Atropa belladonna* L. (Solanaceae). The alkaloid atropine is used to dilate the pupil of the eye. *Atropa belladonna* is a native of Europe and is now cultivated in many temperate regions of India.

(e) **BELLADONA**—It is an old and common drug obtained from the dried leaves, shoots and roots of *Atropa belladonna* L. The dried plant contains several alkaloids of which hyoscyamine and atropine are chief types. Belladonna is used externally to relieve pain of rheumatism, neuralgia, inflammation etc. and internally to check cough, excessive perspiration and intestinal colic.

(f) **COCAINE**—It is obtained from the leaves of *Erythroxylon coca* (Erythroxylaceae). The plant is a native of Peru and Bolivia. Leaves contain a bitter and aromatic alkaloid cocaine used as anesthetic. It is also used as a digestive and nervine tonic.

(g) **CHAULMOOGRA OIL**—It is a fatty oil obtained from the seeds of *Taraktogenos kurzii* King. [Syn. *Hydnocarpus kurzii* Warb, Flacourtiaceae]. It is used in the treatment of leprosy and other skin diseases. The oil is a brownish yellow liquid, it is pressed out of the seeds by hydraulic pressure. Plant is a tall tree with velvety fruits bearing large seeds ; it is a native of Burma and other parts of South-eastern Asia. In India, the plant is found to grow in Assam.

(h) **CROTON OIL**—It is also a fatty oil obtained from the dried ripe seeds of *Croton tiglium* L. (Euphorbiaceae). Plant is a small tree or shrub, native of S. E. Asia, but cultivated in Assam, W. Bengal and S. India. Croton oil is a yellowish-brown liquid with a nauseating odour, used mainly as a strong purgative. In India, flowers and leaves are also used to poison fishes.

(i) **DATURIN**—This poisonous alkaloid is obtained from the roots of several species of *Datura* e.g. *D. metel* L., *D. stramonium* L. etc. belonging to the family Solanaceae.

These species grow everywhere as weeds. Daturin and the dried leaves are used in the treatment of asthma.

(j) **DIGITALINE OR DIGITALIS**—This drug is obtained from the dried leaves of *Digitalis purpurea* L. (Scrophulariaceae). The plant is a beautiful perennial herb, native of Europe, but in India it is cultivated in Kashmir. Digitaline is used as cardiac stimulant and tonic.

(k) **EPHEDRINE** is obtained from stems of *Ephedra gerardiana* Wall. (Ephedraceae, Gymnosperms). Ephedrine is used in the treatment of asthma, colds and hay fever. Plant is a low, leafless shrub with slender green stem; in India it is found to grow in temperate and Alpine Himalayas from Kashmir to Sikkim.

(l) **EUCALYPTUS OIL**—This oil is obtained from the scythe-shaped dried leaves of the plant *Eucalyptus globulus* Labill. (Myrtaceae). The oil is colourless and pungent, it is used in the treatment of nose and throat disorders, asthma, bronchitis and also in perfumery. The plant is also grown as anti-malarial measure for afforestation. Plant is a very tall tree, a native of Australia; in India it is cultivated in Assam, Nilgiri, the Annamalai, the Pulney hills and Simla hills.

(m) **LICORICE OR LIQUORICE**—Liquorice is extracted from the dried roots of *Glycyrrhiza glabra* L. (Papilionaceae). Liquorice is useful in cough, sore throat, bronchitis. It also acts as a diuretic. Plant is a perennial herb, native of the Mediterranean. In India, plant is grown in the Punjab, Jammu and Kashmir, Dehra Dun, Delhi etc.

(n) **NUX-VOMICA**—The well-known drug 'nux-vomica' is obtained from the seeds of *Strychnos nux-vomica* L. (Loganiaceae). Seeds contain two alkaloids viz. strychnine and bucin. Nux-vomica is used as a tonic, stimulant and in the treatment of paralysis and Cochin-China. In India, it is found to grow in Bihar, Orissa, Andhra Pradesh and Madras.

(o) **OPIUM**—It is the dried latex or juice obtained from the unripe fruits of the plant *Papaver somniferum* L. (Papaveraceae). Crude opium is a brownish material containing many alkaloids. Opium has got narcotic and sedative action, hence its derivatives are used to induce sleep, relieve pain and relax spasms. Opium plant is an annual herb with large showy flowers. It is a native of W. Asia, now grown in the Punjab, U. P., Rajasthan and Madhya Pradesh.

(p) **SANTONINE**—The well-known drug 'santonine' is obtained from the dried unopened flower heads of plants *Artemisia absinthium* L., and *A. maritima* L. (Compositae). Santonine is used as vermifuge, stimulant and tonic. The plant is a small perennial herb, native

of W. Asia. In India, santonine plants are cultivated in the western Himalayas from Kashmir to Kumaon.

(q) VASAK—The fresh leaves of the plant *Adhatoda vasica* Nees. (Acanthaceae) are the source of the drug vasak or basak which is used as an expectorant and relieves cough. The plant is an evergreen shrub, found to grow commonly all over India.

(r) KURCHI—It is obtained from the plant *Holarrhena antidysenterica* Wall. (Apocynaceae). The alkaloids obtained from seeds, leaves and bark are used to cure diarrhoea and dysentery. Plant is a small deciduous tree, found to grow in temperate and sub-temperate regions of the Himalayas.

(s) CHIRETTA--The alkaloids obtained from the dried stem of the plant *Swertia chirata* Buch-Ham. (Gentianaceae) is used as a tonic, stomachic and laxative. Plant is a herb, found to grow in temperate Himalayas from Kashmir to Bhutan and Khasia hills.

Narcotic-yielding Plants

Narcotics mean sleep-producing drugs : hence narcotic-yielding plants are those plants inducing drowsiness, sleep and insensibility. Owing to the presence of various alkaloids, some of the plant parts that are smoked or chewed have a distinct stimulating or narcotic effect. Examples of true narcotic-yielding plants are tobacco, opium, cannabis, coca etc. ; they contain alkaloids that are harmful even in small amounts, but used in a large amount may cause stupor, coma, convulsions and even death. Yet human beings in all countries and in all ages have been chewing or smoking various narcotic substances for some physiological effect, for pleasure and more appropriately what should we say to get "some flight from reality"¹.

8.1 Tobacco (*Tamak*, *Tambaku*) : One of the most important world wide commodity is the tobacco. The tobacco plant is a native of tropical America. In India, the use of tobacco originated in connection with religious rites. Tobacco plant was first introduced into Europe in 1556, from there it spread gradually to Africa, Asia and Australia.

Now-a-days, India stands third in the world in the production of tobacco after the U.S.A and China. In India, tobacco is cultivated mainly in Andhra Pradesh, Tamil Nadu, Mysore, U. P., Bihar, West Bengal and the Punjab to some extent. Other tobacco-producing countries are U.S.A., China, W. Indies, USSR, Indonesia, Brazil, Turkey, Italy, Japan, Burma, Ceylon and Bangladesh. In India, about 415 thousand hectares of land are under tobacco cultivation and the annual production of tobacco leaf is about 340 million kg.

Tobacco is obtained from the two species of the genus *Nicotiana*, e. g., *N. tabacum* L. and *N. rustica* L. belonging to the family Solanaceae.

N. tabacum is an unbranched annual herb growing to a height of 0.9-1.8 m. Leaves are large with stout and short petiole, oval. Stems and leaves are provided with glandular hair. Inflorescence cymose, flowers are pink. Fruit is a capsule with numerous small seeds. This species i.e. *tabacum* is the source of *desi* and Virginia tobacco, which is used for cigar, cigarette, pipe mixture, *bidi*, chewing and snuff purposes.

Nicotiana rustica is a smaller plant. Leaves are succulent and round. Flowers are yellow. This species is cultivated for making *hookah*, chewing and snuff tobacco.

¹ Taylor, N. 1949. *Flight from Reality*. Duell, Sloan & Pearce. N. Y.

Climate—Tobacco is grown in all climatic conditions ; specially *tabacum* is cultivated throughout the year while *rustica* is cultivated during cool weather.

Soil—Tobacco can be grown in a variety of soils but normally *tabacum* is grown in a well-drained light sandy loam, low in organic matter, acidic in reaction and rich in mineral matters. *Hookah* tobacco is mainly grown in alluvial soils.

Rotation—It can be cultivated year after year without any rotation ; but in some districts, both *tabacum* and *rustica* are grown in rotation with maize, *bajra*, wheat, barley, *arhar*, groundnut, sorghum etc.

Cultivation—Tobacco is propagated from seeds. Seeds are sown at the rate of 3-5 kg. per hectare in raised or flat well-drained nurseries during August-October, April-May or June-July depending on different types of tobacco in different states. Generally nurseries for raising seedlings are located on sandy or sandy loam soils. Before sowing seeds, nurseries are manured with farmyard manure at the rate of 25-100 tonnes per hectare and ploughed 3-20 times. About a week before sowing, nurseries are again to be manured with N and either castor cake or groundnut cake at the rate of 180 kg. and 90 kg. per hectare respectively. Weeding and thinning operations should be made frequently. When seedlings are 2-3 weeks old, liquid nitrogen may be applied once in a week for a few weeks, followed by a sprinkling of water.

The seedlings, when 6-10 weeks old, are transplanted to the well-prepared (by ploughings 4-6 times) and well-manured (with farmyard manure, N, P_2O_5 , K_2O , castor cake or groundnut cake etc.—the rate of which varies according to the soil conditions) field with a spacing of 84 cm \times 84 cm for cigarette tobacco in A.P., 91 cm \times 91 cm, or 107 cm \times 107 cm for *bidi* tobacco in Gujrat and Mysore and 76 cm \times 51 cm for cigar and chewing tobaccos in Madras. Where the planting is done in dry condition, there transplants are covered with some broad leaves. One or two irrigations after about 4 weeks of planting should be given. Frequent interculturing by means of weeding and hoeing operations is necessary for the better growth of the seedlings.

Topping and Suckering—These two operations are very important regarding the improvement of the size and the quality of leaves. Topping of the crop is done by removing the terminal flower head i.e. inflorescence. Suckering i.e. the removal of growing shoots from leaf axils is also done for a few to several times e.g. once or twice in cigarette tobacco and 8-10 times in *bidi* tobacco ; wrapper tobacco is not topped.

Harvesting and Yield—Harvesting is done when the colour of the leaves changes from green to yellow or yellowish-green. There are two methods of harvesting e.g. (1) *stalk cutting*, in which the entire

plant is cut off and (2) *priming*, in which leaves are only picked one by one from bottom. The time period of harvest differs from type to type. Virginia tobacco is harvested in September-February, 2-2½ months after planting; *bidi* tobacco in January-February, about 4½-5 months after transplanting; cigar and cheroot tobacco in July-September about 3-3½ months after transplanting.

The average yield of tobacco leaf per hectare varies from 750-900 kg. for cigarette; 650-900 kg. for *bidi*; 1,250-1,600 kg. for cigar, cheroot and chewing tobaccos; 800-1,000 kg. for *hookah* tobacco in different States of India.

Curing and Fermentation—Immediately after harvesting, the leaves are simply dried and then suspended in an inverted position from a framework in curing barns. There are two methods of curing, e.g., *flue curing* and *air curing*. Virginia tobacco is flue-cured in small barns—in this process hot air is circulated through *flues* (iron pipes) from a small furnace. This type of curing process takes 100-120 hours to complete. Flue-cured leaves possess a characteristic bright yellow colour. Air-curing is done under natural conditions in well-ventilated barns called *pandals*. Generally cigar and cheroot tobaccos are air-cured. This process takes 12 days.

There are two more methods of curing e.g. *fire curing* and *sun-curing*; in the former case, leaves are dried over fires of wood or charcoal, they are actually smoked without too much increase in temperature—this process is also known as smoke curing; the latter is done in open air under the sun. *Hookah* and chewing tobaccos are cured in these processes.

Grades of Tobacco—On the basis of use, texture, colour, quality etc. tobacco may be graded into following grades :—

1. *Flue-cured*—It is bright tobacco, used for cigarettes, pipes and chewing tobacco.
2. *Fire-cured* -It is used for export, snuff and plug wrappers.
3. *Air-cured*—There are two types, e.g., (a) *Light air-cured* and (b) *Dark air-cured*. Light air-cured tobaccos are used for cigarettes, pipes, chewing and export tobaccos. Dark air-cured is used for snuff, chewing, export and plug tobaccos.
4. *Cigar Filler*.
5. *Ciger Binder*.
6. *Cigar Wrapper*.
7. *Miscellaneous*.

Varieties : The important varieties of tobacco grown in India are :

- (a) *Cigarette* : Delcrest, Virginia Gold, Chatham, Harrison Special.
- (b) *Bidi* : Keliu 49, Keliu 20, Surati 20.
- (c) *Cheroot* : D. R. I.
- (d) *Wrapper* : Dixie-Shade.

(e) *Chewing* : NP 70, NP 35, DP 401.

(f) *Hookah* : NP 18, T 238, C 302.

Diseases and Insect Pests—*Common diseases* :—(1) Damping off caused by *Pythium aphanidermatum*—can be controlled by spraying 1% Bordeaux mixture from the 20th day after sowing; sanitary measures; using raised sand bed nurseries (2) Frog eye leaf spot caused by *Cercospora nicotianae*—can be controlled by treating seeds with silver nitrate solution. (3) Powdery mildew caused by *Erysiphe cichoracearum*—can be controlled by clean cultivating and early priming off leaves, also spraying in the growing stages with 1% Bordeaux mixture. (4) Bacterial wilt caused by *Pseudomonas solanacearum*—control measure same as under potato (refer art. 4.6). (5) Mosaic and leaf curl viruses, can be controlled by maintaining sanitary measures and rouging out diseased plants.

Common insect pests are—Leaf caterpillars (*Prodenia* spp., *Plusia* spp.), cut worms, stem borers (*Gnorimoschema heliopa*) and white flies (*Musca* spp.)—they can be controlled by spraying with 5% DDT, led arsanate or BHC.

8.2 The Indian Hemp (*Ganja*, *Bhang* and *Charas*) : The Indian hemp plant is botanically known as *Cannabis sativa* L. belonging to the family Cannabinaceae. This plant yields *ganja*, *bhang* and *charas*. Indian hemp plant is a native of Asia. In India, *Cannabis sativa* is cultivated in U. P., W. Bengal, Maharashtra, Madhya Pradesh, Tamil Nadu and Orissa solely as a narcotic and drug plant. The use of hemp as a narcotic stimulant is very ancient, probably dates back to 3000 B. C., first in China and later in India. Besides India, hemp plant is now being cultivated in Mangolia, northern and tropical Africa, Asia Minor and other parts of southern Asia. Only the female plant is cultivated for the said narcotics.

The plant is a tall, erect annual under-shrub, dioecious. Leaves simple, stipulate, alternate, palmilobed—lobes lanceolate, serrated. Flowers small, dioecious, unisexual—males in paniced cymes, female in axillary racemes. In male flowers perianth 5; stamens 5, filaments erect in bud. In female flowers, the perianth leaves are connate to form cupular structure surrounding the ovary; carpel one, ovary unilocular with single pendulous apical ovule; styles 2, long, brushy. Fruit a compressed, crustaceous nut. Seeds flattened, with scanty fleshy endosperm and curved embryo.

The dried female inflorescences coated with a resinous exudation form *ganja*, it is used for smoking and in beverages and sweetmeats. In America, *ganja* leaves and flowering tops are rolled into cigarettes and smoked.

Bhang or *siddhi* is obtained by drying the flowering shoots and young leaves of both male and female plants. The decoction of the *bhang* is taken along with water or milk as a drink, it is also smoked; the sticky yellow resin secreted from the flowering tops of the cultivated female inflorescence forms *charas* which is used as an ingredient of many smoking mixtures. Fresh *charas* is dark green in colour which becomes brown in keeping.

The active principle obtained from *Cannabis sativa* is resinous in nature and contains several very powerful alkaloids, these alkaloids

are used in medicine to relieve pain and in the treatment of hysteria and various nervous disorders.

Cultivation of Ganja—*Cannabis sativa* is mainly cultivated for the production of *ganja*. Plants are cultivated in tropical humid climates and on rich, weed-free and well-manured light loamy or sandy soils. Plant is grown as a monsoon crop during June-July. Seeds are sown at the rate of 2.2–4.0 kg. per acre in rows 1.2 metre apart. Thinning is done when plants attain a height of 20 cm. Regular weeding and irrigation should be done wherever necessary. Plant begins to produce flowers during November and the male plants are removed as they produce very little resin.

Harvesting and Processing—Plants are harvested during December-January. Harvesting begins when the lower leaves fall off and the top of the inflorescence begins to turn yellow. The inflorescences are cut, removed to the processing yard and spread out in ridges and furrows. The ridges are levelled down and trod upon to press the floral shoots into compact sheavers. Then the material is dried for sometime, again trodden and turned over at regular intervals. They are then collected and arranged in a flat circular heap (called '*chakki*') of 0.6-0.9 m in height. Next, the compacted mass is kept under pressure for 2-3 days to initiate chemical changes; then heaps are broken up, again turned over and spread out in a thick layer. On the fourth day, the *ganja* becomes ready for storage in special sheds.

Yield and Types—The average yield of *ganja* per acre varies from 115-200 kg. There are two varieties of *ganja* viz. the flat or Bombay *ganja* and round or Bengal *ganja*.

Fibre-yielding Plants

With the advancement of civilization fibre-yielding plants stand second to food plants in their usefulness to man. Next to food and shelter, man needed some form of clothings made from the fibres of stems, leaves, fruits and roots of many plants. From the very beginning of civilization, plant fibres have had a more extensive use than animal fibres like wool, fur and silk. Gradually the use of vegetable fibres for various purposes has increased greatly. There are numerous species of fibre-yielding plants, of which the greater number comprising native species used for various purposes by local people in all parts of the world.

On the basis of their utilization, Hill (1952) has classified fibres into the following six groups :—

(a) *Textile fibres*, used in textile industry in the manufacture of fabrics, netting and cordage.

(b) *Brush fibres*—These are tough and stiff fibres, used in the manufacture of brushes and brooms.

(c) *Plaiting and Rough weaving fibres*—These are flat, pliable fibrous strands which are used in making baskets, chair seats, straw hats, sandals etc.

(d) *Filling fibres*—These fibres are used for stuffing cushions, mattresses etc.

(e) *Natural fabrics*—These are tree basts which are used sometimes as substitutes for cloth or lace.

(f) *Paper making fibres*—Generally these are wood fibres and textile fibres used in either the raw or manufactured state.

Fibres are mostly sclerenchyma cells, although they differ in texture, strength and chemical composition. Cells are long, thick-walled and with pointed ends ; the walls contain cellulose and lignin. According to the origin of fibres, fibres may be bast fibres, wood fibres, sclerenchyma cells associated with vascular strands in leaves, surface fibres developing as hair-like outgrowths on the seeds etc. There are lots of fibre-yielding plants belonging to different families ; of these more important families are Tiliaceae, Malvaceae, Bombacaceae, Leguminosae, Moraceae, Urticaceae, Linaceae, Musaceae, Bromeliaceae, Liliaceae, Agavaceae, Palmae etc.

9.1 Cotton (*Karpas*, *Kapas*) : It is the oldest and greatest industrial crop of the world. In India, cotton has been in use since 1800 B.C. Cotton was introduced in Europe from India by Arabians. The word 'cotton' has been derived from the Arabic term '*qutn*'.

Before independence, India was the second largest cotton producing country in the world. Since partition, the area under cotton cultivation is 19 million acres and the average production of cotton is estimated at 57 lakh bales. Now-a-days United States leads in production with 14,868,000 bales (approx.) followed by India, Pakistan, Soviet Union, Egypt, Brazil etc. The chief cotton exporting countries are U.S.A., India, Egypt and Brazil while Great Britain, Germany and Japan are importing cotton.

Varieties or Kinds of Cotton—Cotton is the *surface fibre* obtained from four major species of the genus *Gossypium* belonging to the Family Malvaceae. Four species of cultivated *Gossypium* are :

(1) *Gossypium arboreum* L.—This species is diploid ($2n=26$ chromosomes) and forms the *desi* cotton of India. It is also grown in Arabia and Africa. The staple is coarse, very short (about 9.5 mm—19.05 mm in length) but strong. This cotton was probably the first to be used commercially.

Plant is a perennial tree. Leaves palmately lobed, lobes mucronate. Flowers axillary, large, solitary on jointed peduncles ; bracteoles 3, large, leafy, cordate. Calyx cupular, truncate or slightly 5-toothed. Petals 5, connate at base. Stamens numerous, monadelphous forming a staminal column, anther one-celled. Ovary 5-chambered, style clavate, 5-grooved at the apex, stigmas 5 ; ovules many in each chamber. Fruit capsule, capsule oblong, pointed. Seeds free, covered with white wool overlying a dense green down.

(2) *Gossypium herbaceum* L.—This species is also diploid ($2n=26$ chromosomes). It is the chief cotton of Asia and also forms *desi* cotton. In India, this species has been growing since time immemorial. It is utilised for low quality fabrics, carpets, blankets etc. and for blending with wool ; cottons obtained from this species are generally coarse and short to medium stapled.

Plant is an annual shrub, sub-glabrous or hairy. Leaves cordate, 3.5 or 7-lobed, lobes broadly acuminate. Flowers yellow with purple centre, rarely yellow or white or purple, petals spreading, calyx truncate, obovate or cuneate ; bracteoles equalling the capsule, not divided below the middle. Capsule ovate, globose, mucronate, 3-5 valved. Seeds 5-7 in each cell, ovoid. Cotton white, rarely brownish, overlying a greenish or greyish down.

(3) *Gossypium hirsutum* L.—It is a tetraploid ($2n=52$ chromosomes) and new world species. It is a native of America and constitutes American and Cambodia cotton and is commonly called upland cotton. Upland cotton constitutes the greater part of the cultivated cotton of the world. The fibres are fine and white, staple length ranges from 6.2 mm to 25.7 mm.

This species is characterised by the following characters. Flowers are *white or light yellow* and *unspotted*. Fruits or bolls as these are called, are *4 or 5-valved*. *Seeds are fuzzy all over*.

Other characters are like those of *G. arboreum*.

(4) *Gossypium arboreum* L. var. *nadam* (Watt) Prokh. (Syn. *G. barbadense* L.)—This is also a new world and tetraploid ($2n=52$ chromosomes) species. The native home of this species is probably South America. Under this species, there are two distinct types of cotton e.g.

(a) *Sea-island Cotton*—Purely cultivated form. Fibres are fine, light cream coloured, strong, regular in the number and uniformity of twist and silkier in appearance. Staples range in length from 33.0 mm to 50.8 mm or more. Sea-island cotton was introduced in U. S. A. from West Indies in 1785. In India, another variety under this, known as *Andrews* having extra long staple can be cultivated successfully in the costal areas of Kerala and Mysore. This variety is susceptible to a large number of pests and diseases and very sensitive to environmental conditions.

(b) *Egyptian Cotton*—It is grown mainly in Nile basin of Egypt, and was introduced from Central America. In appearance, this plant is very similar to sea-island cotton and is probably of hybrid origin. Staples are brown in colour and somewhat shorter than sea-island cotton, measuring from 25.7 mm to 26.1 mm. This cotton is used for hosiery, tyre fabrics and fine dress materials.

Plants are perennial shrubs or tall herbs, branches purplish. Leaves nearly glabrous, cordate, 3-5 lobed; lobes oblong acuminate, bracteoles very large, deeply gashed; stipules linear-lanceolate.

Flowers are *bright yellow with purple spots*. Petals convolute. Ovary ovoid, pitted, 3-5 celled.

Fruits or bolls are oval acuminate, 3-valved. Seeds are *fuzzy only at the ends*, black, free or coherent.

Characteristics of Cotton—Fine fibrous hairs occur on the surface of the seeds¹—these fibrous hairs constitute the raw materials of the industry. Hairs are flattened, twisted and tubular which compose the *staple, lint* or *floss*—the length and qualities of which vary in different species.

Climate—Cotton is mainly a sub-tropical fibre crop. It grows well in areas where rainfall ranges from 762.0 mm to more than 2,540.0 mm per annum. Sufficient rainfall is required during early stages of growth. For better growth average temperature requirement varies from 43°C to 46°C. Cotton can grow in drier areas provided it is irrigated.

¹ These hairs are unicellular outgrowths from the epidermis of the seed. In the cultivated cottons there are two types of hairs, viz. (a) *Lint* :—the hairs grow long, in cross section there is a lumen due to reduced deposition of cellulose; the deposition of cellulose takes place in a spiral manner, with changes in the direction of deposition—the resulting convolutions permit spinning. The lint is easily detachable from the seed (b) *Fuzz* :—the hairs are shorter, the central cavity or lumen is almost closed due to cellulose deposition. These hairs are strongly attached to the seeds and cannot be spun. Only the lint is of commercial or economic importance.

Soil—Cotton grows best in sandy soils in damp, humid regions that are nearer to water. It grows well also in Indo-Gangetic alluvium, the black cotton soils of Central and Southern India and the red laterite soils of other parts of India.

Rotation—Cotton is normally grown in rotation with other crops ; the common rotations, in different parts of India, are *cotton-wheat*, *cotton-legume-wheat*, *cotton-jowar*, *cotton-bajra*, *cotton-sesamum*, *cotton-ragi* etc. In some places cotton is grown mixed with some crops like maize, jowar, sesamum, pulses, vegetables, groundnut etc.

Cultivation—According to variety, climate, soils etc., cotton cultivation varies from tract to tract.

Seeds are generally sown by broadcasting at the rate of 2.2–9.0 kg. per acre during April-July.¹ Practice of sowing seeds in rows with the help of drills or metal container attached to a plough is also done, in this case spacing varies from 30.5–152.0 cm between rows and from 15.2–45.0 cm within the row. Before sowing cotton seeds are treated with different types of chemical reagents or mud or cowdung due to the fuzziness² of seeds.

Before sowing, the land is given one or two ploughings (in Tamil Nadu and in some parts of North India where irrigated cotton follows wheat). The black cotton soil of Central and Western India is not ploughed but is harrowed three or four times, in this case ploughing is done only once to remove the weeds. Weeds are also removed by the help of hand-hoes in some places.

Generally, cotton is not manured sufficiently, but if the crop is properly manured, the yield is increased. Any leguminous crop may be grown as a green manure or as a crop in rotation preceding cotton. For irrigated crop a balanced fertilizer mixture of 13.5 kg.-27.0 kg. N, 9 kg.-18 kg. P_2O_5 and 9 kg.-18 kg. K_2O per acre is recommended. For rainfed i.e. unirrigated cotton, half the dose is sufficient.

Cotton is mainly an unirrigated i.e. rainfed crop. Irrigation is required where the rainfall is insufficient. Watering is required at the time of flowering and fruiting stage. For the maturation of bolls, sufficient soil moisture is necessary.

Harvesting—Cotton is harvested in three or four pickings after the maturity of bolls. The harvesting usually starts in October and extends up to March-April. The *Kapas* i.e. seed-cotton is removed from the bolls in the field. In case of closed-boll cottons, partially open bolls are collected from the plants in the field.

Yield—Depending on the agro-climatic conditions, the yield varies from tract to tract. In dry areas, the yield varies from 20 kg.-50.5 kg. of lint per acre ; in irrigated areas it varies from 90.5 kg.-113 kg.

¹ Some varieties are also sown during August-September.

² Besides lint or staple the testa bears another type of short, coloured or white fibres strongly attached to it—this is known as fuzz.

Marketing and Processing—*Kapas* or seed-cotton is sold by farmers to agents of ginning mills or to village merchants.

Next several operations are necessary in order to prepare the raw cotton fibre for use in textile industry. These operations are :— (a) *ginning*—here *Kapas* is ginned in either saw-toothed or roller gin machine ; (b) *baling*—here lint or staple is packed either in loose or compressed bales ; (c) *transporting mills*, (d) *picking*—a process in which machine removes foreign matter and delivers the cotton in a uniform layer : (e) *lapping*—in this operation three layers are combined into one : (f) *carding*, *combing* and *drawings*—in these operations the short fibres are extracted, other fibres are straightened and evenly distributed and finally (g) *twisting* the fibres into threads.

The Uses of Cotton—Now-a-days cotton forms the most important article of commerce. Cotton is mainly used, either alone or in combination with other fibres, in the manufacture of textiles of various types. It is also used in the manufacture of rubber-tyre fabrics ; unspun cotton is used for stuffing cushions, pillows, mattresses, pads etc. Absorbent cotton, being pure cellulose, is used as one of the raw materials in cellulose industry. Mercerized cotton which is very highly priced, is made by treating fibres with caustic soda—this cotton imparts high lustre and silky appearance and thereby used in the manufacture of top grade textiles and also in combination with synthetic fibres like terylene, nylon etc.

Cultivated Varieties of Cotton :—

Some of the improved varieties of cotton grown in India are :—

- (i) Punjab : 320F, LL 54, H. 14 (*hirsutum*), 231R (*arboresum*)
- (ii) U.P. : 216F, 320F (*hirsutum*), Raniben (*arboresum*)
- (iii) Rajasthan : 320F, C. Indore-1, 134-Co. 2M (*hirsutum*), Ganganagar-1, Virnar (*arboresum*), Digvijay (*herbaceum*)
- (iv) M.P. : Badnawar-1, Narbada (*hirsutum*)
- (v) Gujrat : Kalyan, Digvijay, Vijalpa (*herbaceum*), Devitej, Deviraj, (*hirsutum*), Senjay (*arboresum*)
- (vi) Maharashtra : Virnar, Gaorani 22 & 46 (*arboresum*), Buri 147, Deviraj (*hirsutum*)
- (vii) Andhra Pradesh : Parbhani american, Laxmi (*hirsutum*), Gaorani-6, Cocanadas-2, Nandicum, Adonicum (*arboresum*)
- (viii) Mysore : Andrews (*barbadense*), Jayadhar, Sel 69 (*herbaceum*), Laxmi, 170-Co-2, M. A, 5 (*hirsutum*), H 420, Gaorani-22 (*arboresum*)
- (ix) Tamil Nadu : 216F, MCU-2, 3, 4 & 5 (*hirsutum*), Pandyan (*arboresum*) Sujata (*barbadense*)
- (x) Kerala : Andrews (*barbadense*)

Diseases and Insect Pests—

Common diseases are—(1) Anthracnose caused by *Glomerella gossypi* and *Colletotrichum indicum*—it can be controlled by (a) treating seeds with organomercurials before sowing, (b) spraying the crop with 1%, Bordeaux mixture and (c) destroying infected plants. (2) Black arm or angular leaf spot caused by *Xanthomonas malvacearum*—it can be controlled by growing resistant varieties and treating seeds with organomercurials @ 2 grams per kg. or with sulphuric acid.

(3) Dry-rot or Sore shin caused by *Macrophomina phaseoli*—can be controlled by crop rotation practice and growing resistant varieties. (4) Leaf spot caused by *Mycosphaerella gossypina*—controlled by growing resistant varieties. (5) Powdery and Grey mildew caused by *Leveillula taurica* and *Ramularia areola* respectively—respective control measures are dusting crop with powdered sulphur @ 6.7 kg. per acre and with 1% Bordeaux mixture. (6) Wilt caused by *Fusarium vasinfectum*—controlled by growing resistant varieties.

Common insect pests are—(1) Cotton spotted bollworm (*Earias* spp.)—control by removing and destroying all attacked shoots and bolls and spraying with 0.03% Endrin @ 360–425 litres per acre at 15 days intervals. (2) Cotton stem borer (*Sphenoptera gossypii*)—can be controlled by burning and uprooting withered plants. (3) Cotton stem weevil (*Pemphres offinis*)—can be controlled by preventing the cultivation of other food plants in off season. (4) Cotton white fly (*Bemisia tabaci*)—can be controlled by spraying with 0.25% BHC or 0.03% Endrin @ 360–425 litres per acre. (5) Cotton bugs (*Dysdercus* spp.)—can be controlled by dusting with 5% BHC @ 6.7–9.0 kg. per acre. (6) Cotton leaf-roller (*Sylepta derogata*)—controlled by picking and destroying rolled leaves, and also by spraying crop with 0.25% DDT or BHC @ 360–425 litres per acre, or dusting with 5% DDT or BHC @ 6.7–9.0 kg. per acre.

9.2 Jute (Pat, Jute): Next to cotton, jute forms the most important fibre crop used more extensively for various purposes.

Jute, although a native of Malaya or Ceylon, is now almost entirely an Indian crop. In India, jute is grown in the States of North-East India e.g. W. Bengal, Bihar, U. P., Orissa, Assam, Tripura and Manipur. The crop is cultivated on about 0.90 million hectares annually, the annual average production of dry fibre is about 6.3 million bales of 181 kg. each.

Jute is also cultivated in large scale in Bangladesh; besides India and Bangladesh, other countries like Brazil, Mexico, Japan, China U.A.R., Argentina, Indonesia, Iran etc. cultivate jute.

The earliest record of the use of jute fibre in India as a sac-cloth is known from the time of the Mughal Emperors.

India not only grows most of the jute, but is the largest manufacturer and exporter of jute products. About 25% of the annual production is exported to Great Britain, U.S.A. Belgium, Germany, France and Italy; 67% of the annual production is consumed in India by jute mills and the rest is retained by the growers.

Jute is a *bast fibre* obtained from the secondary phloem of two species of the genus *Corchorus* belonging to the family Tiliaceae. Two species of *Corchorus* are (a) *C. capsularis* L. and *C. olitorius* L.

(a) *Corchorus capsularis* L.—Jute, white jute; *pat* or *tita-pat*. It is a lowland species. Plant is an annual under-shrub reaching up to a height of 3–6 m. Stem branched or unbranched. Leaves stipulate, glabrous, 5–13 cm × 2.5–8.2 cm, ovate-oblong. Flowers in extra-axillary cymes in groups of 2–5 or more, smaller (0.3–0.5 cm in length). Sepals 5, coloured or green, petals 5, yellow or pale yellow; *stamens* 20–30; ovary rounded, 5-carpelled, ovules usually 10 in each loculus in two rows, styles 2–4 mm, stigmas 2–3 fid, pubescent. Capsule rounded, 1–1.5 cm in diameter, wrinkled, rarely smooth,

muricate, 5-locular ; seeds 7-10 in two rows in each loculus, without transverse partitions. Seeds oval, small, chocolate brown.

(b) *C. olitorius* L.—Jews mallow or Tossa jute ; *Koshta* or *mitha-pat*. It is an upland species. Plant is an annual under-shrub growing up to a height of 4.5 m. Stem branched. Leaves stipulate, stipules larger than capsularis ; glabrous, 7-18 cm × 4-8 cm, oblong. Flowers in extra axillary cymes in groups of 2.5, about 1 cm in length, larger than capsularis. Sepals 5 or 6, coloured or green ; petals 5 or 6, entire or splited, yellow ; stamens 30-60 ; ovary elongated, 5 or 6 carpelled, ovules usually 40 in each loculus in one row ; styles 3-5 mm ; stigma globular, entire, pubescent. Capsule long cylindrical, 6-10 cm long, 0.3-0.8 cm in diameter, ridged lengthwise, 5-6 locular ; seeds 25-40 in single row in each loculus with transverse partition between each seed. Seeds pyramidal in outline, smaller than capsularis, bluish-green to steel-grey or even black in colour.

Climate—Generally warm and humid climate with temperature ranging from 24°C to 35°C and 90% relative humidity favour the growth of jute plants. Untimely rain, continued drought, stagnant water are harmful but the plant can stand flooding to some extent at later stage of growth.

Soil—Jute can be grown on almost all types of soil, which are neither very heavy clay nor very sandy, with proper depth, provided with favourable temperature and well distributed rainfall. Loamy alluvial soil with deposits of fertile silts from flood water is the best for jute cultivation.

Rotation—Jute can be grown alone for years together or in rotation with paddy and pulses. On lowland, jute-fallow-paddy (*aman*) constitutes the normal rotation. On highlands, the crop is grown in rotation with pulses (like gram, pea etc.), potato, wheat, barley, oat, mustard or paddy.

Cultivation—Jute seeds are very small ; for this, jute requires a clean and clod-free seed bed. Therefore, the land is ploughed and cross-ploughed for several times (5-6 times at least) ; then, after each operation, the land is beamed (laddered) for breaking up the clods.

Additional manuring is not required in soils receiving fresh silt every year or soils which are already well-manured for crop preceeding jute. In other soils, 40-80 q/ha. of well-rotten cattle manure or compost and 455 kg./ha. of weed or wood ash are generally used before sowing during the preparation of land ; this is followed by a top dressing of 60-120 kg./ha. of ammonium sulphate to the 4-6 weeks old crop. Old alluvial soils should be manured with 35-65 kg./ha. of nitrogen in two doses i.e. half of the amount before sowing and the other half a week after the germination of seeds. Sometimes potash and lime are also used.

In lowlands, sowing is done in February while medium and highlands are sown in March-April and May-June respectively. The

seeds are generally sown by broadcasting at the rate of 7.5 kg. per hectare for *olitorius* variety and 12 kg. per hectare for *capsularis* variety or seeds are dropped in shallow furrows (3.5 cm deep) behind the plough. Now-a-days, line sowing with seed drills has been greatly adopted. In this practice seeds at the rate of 4.5 kg. (for *olitorius* variety) or 6-7 kg. (for *capsularis*) per hectare are sown in rows with a spacing of 30.5 cm between the rows and 5.0-7.5 cm within the row. When the seedlings attain a height of 7.5-22.8 cm, then the crop is lightly hoed with *bida* or *achra*; subsequently two or three hand weedings are given and the crop is gradually thinned to a spacing of 9-10 cm between plants.

Harvesting—The crop is generally harvested within three or four months after planting while the flowers are still in bloom, but right stage for harvesting purpose is a little later when pods begin to appear. Depending on the time of sowing and the variety grown, the harvesting period varies from June to October.

At the time of harvesting, plants are cut at or near the ground level; in case of flooded land, plants are uprooted. The harvested plants are usually left on dry land for a few days (2-3) for the shedding and the drying up of the leaves, then tied in bundles and kept covered with green leaves, weeds and earth for 3-4 days. After this, the bundles are shaken to remove the covering debris and transferred to water for retting.

Retting or Steeping and Stripping—Bundles are retted or steeped in gently flowing, fairly deep, clean, soft and tepid water for 10-15 days in July-September to rot out the softer gummy tissues; sometimes, retting may take 25 days or more, specially when the temperature of water is low. In this process, complete submergence of stalks is essential; to ensure proper retting of the root end, the bundles with their root ends are generally kept in water for 2-3 days before entire bundles are fully submerged.

After retting is complete, the stalks are stripped. In this operation, known as 'beat-break-jark' process, 8-10 stalks are taken at a time, their root ends beaten with a wooden or bamboo mallet until the fibres are loosened. Loosened fibres are then wrapped round the fingers and the stalks or stems are jerked forward and backward over the surface of water till the fibre is completely separated. The separated fibre is then rinsed, washed, cleaned, wrung and piled on the ground. Finally, strands are opened out and dried in the sun for 2-4 days and tied into bales ready for the market. The fibre content of the plant varies from 4.5-7.5 per cent.

Yield—The average yield of the variety *capsularis* varies from 9.0-13.5 quintals of dry fibres per hectare and of the variety *olitorius* 13.5-18.8 quintals.

Characteristics of Fibres—The best fibre shows pale-yellow colour and silky lustre; the length varies from 1.8 to 3.0 m and is very stiff due to lignification.

Uses of Jute—Jute is used mainly for rough weaving. Various types of bags *viz.* gunny, burlap etc., wool, potato sacks and the covers of cotton bales are made from jute. The superior long and glossy fibres are used for making carpets, twine, curtains, coarse cloth etc. Jute butts *i.e.* short fibres and pieces from the lower ends of the stalks are used in paper making.

Varieties : Both the species of *Corchorus* *i.e.* *C. capsularis* and *C. olitorius* are grown commercially. *C. capsularis* is a highly adaptable and hardy species, growing well in both low and highlands. The leaves of *olitorius* are sweet and edible while *capsularis* has bitter leaves. Many improved varieties of jute have been released for cultivation ; important among these are :

Capsularis : D-154, JRC-212, JRC-321, JRC-5854 etc.

Olitorius : Chinsurah Green, JRO-632, JRO-620, JRO-7835, JRO-878 etc.

Diseases and Insect Pests :

Common diseases are :—(1) Seedling blight, Stem rot, Root rot, Collar rot—all caused by *Macrophomina phaseoli*. Control measures are : (a) seed treatment with organo-mercurial (e.g. Agro-san GN., Ceresan etc.) or non-mercurial (Captan) compounds ; (b) clean cultivation ; (c) crop rotation. (2) Wilt—the primary and secondary pathogens are *Macrophomina phaseoli* and *Fusarium solani* & *Pseudomonas* sp. respectively. Complete control measures are yet unknown, but changing the cropping pattern with various crop rotations and proper drainage of the field may restrict incidence. (3) Anthracnose—in *C. capsularis* it is caused by *Colletotrichum corchorum*, while in *C. olitorius*—two pathogens *viz.* *Colletotrichum gleosporioides* and *Phomopsis* sp. are associated. May be controlled by use of resistant varieties, seed treatment, copper spray and restricted use of Nitrogen fertilizers. (4) Soft rot caused by *Sclerotium rolfsii* (= *Pellicularia rolfsii*)—control measures consist of clean cultivation, deep ploughing and Copper Oxchloride spray. (5) Die-back or Black-band—caused by *Diplodia corchori*—control measures are not yet known.

Common insect pests are : (1) Jute semilooper (*Anomis sabulifera*)—it can be controlled by (a) removing the larvae, (b) spraying with 0.5% BHC @ 130–225 litres per acre or dusting with 5% BHC @ 4.5–9 kg per acre (2) Hairy Caterpillar (*Dicristia obliqua*)—may be controlled by (a) plucking the infested leaves in the early stage, (b) by spraying with Parathion (0.03–0.04%) or Endrin (0.04–0.05%) or Endosulfan (0.04%). (3) Jute stem weevil (*Apion corchori*)—the control measures are treating with DDT (0.25%) or Endrin (0.03%). (4) Indigo Caterpillar (*Spodoptera exigua*)—may be controlled by dusting 10% BHC @ 4.5–5.5 kg/acre. (5) Termites (*Microtermes* sp.)—the control measures are (a) avoiding repeated cultivation of jute in the infected land, (b) treating the soil with Aldrin dust (5% @ 40 kg/ha). Among the non insect pests Yellow mite (*Hemitarsonemus latus*) is very destructive. It can be controlled by (a) dusting lime sulphur (3 : 1) @ 20 kg/ha or (b) spraying Endosulfan 0.2% @ 3 ml./5 litres water.

9.3 Flax (the Linseed plant) : Flax or *Alsi* is also another useful and valuable fibre which stands second to cotton in importance. Flax fibre is finer and superior to cotton ; it forms the *linen* fibre of commerce.

The use of flax dates back to the time of Swiss Lake Dwellers—the oldest people in Europe. It was also well known to the Hebrews and the Egyptians. Egyptians used linen as clothings and also for their mummy cloths.

In India, flax is grown generally in temperate regions of U. P., Madhya Pradesh, Maharashtra, Bihar and W. Bengal. In India,

flax is cultivated mainly for the oil contained in the seed rather than fibre obtained from the stem. In western countries, flax is grown specially as fibre crop.

Flax is the bast fibre, obtained from the plant *Linum usitatissimum* L. belonging to the family Linaceae.

Flax plant is an annual herb, reaching up to a height of 1·2 m. Leaves are small, alternate, simple, linear or lanceolate, exstipulate, entire. Inflorescence cymose or solitary. Flowers are blue or white, regular, hermaphrodite. Sepals 5, imbricate. Petals 5, contorted, fugacious. Stamens 5, disk gland opposite the petals. Carpels 5, united. Ovary 5-chambered, each chamber 2-locellate; styles 5, usually free, stigmas clavate or capitate; ovules 10 in each locellus. Fruit a 5-celled capsule. Seeds compressed.

Climate—Flax is mainly a crop of temperate regions. Its cultivation is restricted in plains but can be grown up to an altitude of 765 m. For better growth, flax requires an average annual rainfall ranging from 274·0 mm to 762·0 mm and cool climate.

Soil—For fibre crop it grows best in soils rich in moisture and organic matter. It also grows well on deep clayey black soils and alluvium loams.

Cultivation—Fine, porous and firm seed bed is prepared by ploughing several times followed by harrowing and planking. Seeds are sown in seed bed either by drilling or broadcasting at the rate of 36·0-54·5 kg. per acre. Seedlings are transplanted in a well prepared land and the spacing between lines is normally maintained between 22·8 and 30·5 cm. The crop does not require any interculture operations except one or two irrigations in case of late sown crops. Three to four irrigations are also required when the crop is cultivated in dry condition.

Harvesting—It is usually done by hand. The crop is harvested by the end of January or early February before the capsules are mature. Harvested stalks are allowed to dry in the field for one or two days. Then stalks are broken and seeds from them are removed by a process known as *ripping*. De-seeded stalks are then retted.

Retting—Retting is done by submerging the stalks in water or exposing them to dew. Depending on the temperature and softness of the water, the time for retting varies from 2 to 3 weeks. In this process, fibres become free from other tissues of the stalks due to enzymatic action. After retting, the straw is dried in sun and cleaned; next by means of *scutching* process fibres are completely separated from longer fibres either by hand or by a hackling machine.

Characteristics of Flax Fibres—Flax fibres are very fine, durable and short. The length of the fibre varies from 0·4 m to 0·6 m, the colour varies from creamish-white to gray. Fibres have great tensile strength.

Uses—Flax fibres are mainly used in the manufacture of fine fabrics e.g. linen, cambrics, hollandes etc. and linen threads. Fibres are also used in the manufacture of canvas, carpets, fish nets, cigarette paper, wrapping paper, insulating materials, twines etc.

Diseases and Insect Pests—

Common diseases are : (1) Rust caused by *Melampsora lini*—it can be controlled by growing resistant varieties and treating seeds with Agrosan GN @ 2 gms per kg. before sowing. (2) Wilt caused by *Fusarium lini*—control measures are as under (1). (3) Anthracnose or Canker caused by *Colletotrichum lini*—control measures are same as under (1). (4) Alternaria blight caused by *Alternaria lini*—it can be controlled by treating seeds with Agrosan GN before sowing and also by growing late varieties.

Common insect pests are : (1) Cut worm (*Agrotis* spp.)—can be controlled by treating soil with 5% DDT before sowing @ 9.0–11.3 kg. per acre, by dusting the base of plants with 5% DDT @ 9.0–11.3 kg. per acre. (2) Aphid (*Myzus persicae*)—can be controlled by spraying with 0.2% BHC or 0.05% nicotine sulphate @ 130–212 litres per acre. (3) Linseed gall midge (*Dasyneura lini*)—it can be controlled by growing of early varieties and mixed cropping and also by spraying with 0.2% DDT @ 40–50 gallons per acre.

9.4 Sunnhemp, San or Sunn (*Shan, Patua*): Sunnhemp is another important fibre plant. The fibre obtained from the stem is a bast fibre. It is grown extensively in various States of India e.g. Tamil Nadu, Andhra Pradesh, U.P., Madhya Pradesh and Bihar; sunnhemp is also cultivated in Ceylon and some regions of southern Asia. In India, the annual area under the cultivation of sunnhemp crop is little over 240 thousand hectares. The annual production is about 80,000–100,000 tonnes. About 20–30 percent of the total production is exported, mainly to U.S.A., U.K. and Belgium. Sunnhemp is also known as Bombay hemp. Sunnhemp, probably, is the first known fibre plant—the reference of which is mentioned in Sanskrit writings.

Crotalaria juncea L. is the botanical name of the sunnhemp plant, it belongs to the sub-family Papilionaceae of the family Leguminosae.

Plant is an annual tall shrub. Branches erect, branchlets rounded. Leaves simple, lanceolate or linear, stipules minute along the twigs or absent, obtuse. Inflorescence raceme—either terminal or lateral. Flowers yellow, papilionaceous, irregular, hermaphrodite, perigynous. Sepals connate in a short tube, teeth 5, imbricate. Petals 5, free, vexillary exceeding calyx—standard orbicular, wings shorter, ovate-oblong; keel broad. Stamens 10, monadelphous. Ovary sessile and oblong.

Climate—Plants thrive best in tropical and sub-tropical climate having an average rainfall ranging from 50–70 cm per annum.

Soil—For fibre, plants require light, well drained alluvial loams, red loams and light to medium black soils.

Rotation—Plants are grown alone in rotation with various food crops, oil-seeds, cotton etc.

Cultivation—The crop is either grown as *kharif* crop dependent

on monsoon rains for fibre purposes or as *rabi*-crop in paddy lands for manurial fodder purposes.

Just after the first monsoon rains, or after an irrigation (for *rabi* crop) 2-3 ploughings followed by harrowing are given to the land for a good tilth. Normally, manuring is not done. The sowing of the *kharif* and *rabi* crops is done in June-July and September-October respectively. Seeds are sown by broadcasting or with the help of drills in rows 30 cm apart at the rate of 68-90 kg. per hectare.

Harvesting—The fibre crop is harvested within four to four and half months after planting either in pod formation stage (in U.P. and Madhya Pradesh) or in the full bloom stage (in Deccan). At the time of harvest, plants are either pulled out or their stems are cut very close to the ground.

Retting and Stripping—Harvested plants are left on the ground for a few days for drying up and shedding of their leaves, flowers, pods etc. The stalks are then tied in bundles; next for retting purpose such bundles are retted in clear, stagnant or slow running water and kept submerged for a week. Immediately after softening of stalks, their lower portions are broken and fibre peeled by stripping upwards. Then the stripped fibres are cleaned in water by lashing, dried in sun for 2-3 days, twisted in hands and tied into bales ready for the market.

Uses—The fibre is stronger than jute and lighter in colour but somewhat coarse and more enduring. It is used for making coarse canvas, nets, ropes, twines, sacks, cordage etc.

Yield—The fibre content of the dry stalks lies between 7-8%. The average yield of the fibre varies from 500 to 900 kg. per hectare.

Diseases and Insect Pests—Common diseases are : (1) Powdery mildew caused by *Oidium erysiphoides*—control measure is same as under cotton. (2) Wilt caused by *Fusarium udum* var. *crotalariae*—can be controlled through resistant varieties, crop rotation and crop sanitation. (3) Rust caused by *Uromyces decoratus*—control is not known. (4) Anthracnose caused by *Colletotrichum curvatum*.

Common insect pests are : (1) Hairy caterpillar (*Utetheisa pulchella*)—can be controlled by destroying eggs and caterpillars in the early stage, also dusting with 5% BHC @ 6.7–9.0 kg. per acre. (2) Stem borer (*Laspeyresia pseudonectis*.)

9.5 Mesta (Patsan or Ambari) : Mesta is also known as Bimlipattam jute or Deccan hemp. In India, mesta is grown in many States viz. West Bengal, Bihar, Assam, Andhra Pradesh and the Punjab and the total annual area under cultivation is 380 thousand hectares.

Mesta is grown for bast fibre, it is obtained from the stem of *Hibiscus cannabinus* L. belonging to the family Malvaceae. It is probably a native of tropical and sub-tropical Africa.

Plant is a herb with straight, glabrous, prickly stem. Leaves simple, lobed and stipulate. Flowers axillary solitary; bracteoles 5, without any appendages on the back, adnate to the base of calyx

tube. Calyx 5 lobed, dry, horny in fruit, lobes prickly and with prominent midrib having a large gland. Petals 5, connate at the base and adnate to staminal column. Stamens many, monadelphous, anthers reniform, one-celled, filament short. Carpels 5, united; ovary 5-chambered; ovules 3 or more in each chamber; styles 5, connate below, stigmas capitate. Fruit a loculicidally 5-valved capsule. Seeds glabrous.

Climate—Mesta grows well in areas where the rainfall continues for 4-5 months and the annual average rainfall ranges from 50 to 75 cm.

Soil—It is grown on variety of soils e.g. light black soil, sandy alluvial loams, laterite and gravelly soils, but grows best on a well drained, sandy loam soil, rich in humus.

Rotation—Normally, mesta is grown mixed with pulses, bajra, jowar, *kharif* cotton etc. Sometimes it may be grown alone in rotation with cereals, pulses and other crops.

Cultivation—To obtain a well pulverised seed bed for pure crop, two to three ploughings and cross ploughings followed by harrowing are given to the land. Manure is rarely applied, but an application of 25-35 kg. of nitrogen per hectare either in organic or inorganic form gives a good yield. The seeds of pure crop are sown from May to July either by broadcasting or by drill in rows 20-30 cm apart. A few hoeings are given and the crop is thinned if necessary.

Harvesting, Retting etc.—Mesta plants are harvested in flowering stage. Plants are uprooted, then dried in sun for a few days and tied in bundles; in the meantime leaves, flowers and fruits, if formed, are removed. Then the bundles are placed with their root ends down in water for 2-3 days to soften the harder parts of stalks. Next, stalks are steeped or retted horizontally in water for 10-20 days. When retting is complete, fibres are stripped off from the stalks by beating with a mallet, then loosened fibres are wrapped round the fingers and the stalks are agitated in water till fibres are completely separated. Separated fibres are then cleaned in water and piled on the ground.

Yield—The fibre content of dry stalks is about 16 per cent. The yield of the fibre from pure crop varies from 9 to 13 quintals per hectare.

Uses—Fibres of mesta are used for making rough canvas and sack-cloth, fishing nets, cordage etc. It is often used in admixture with jute fibres in manufacture of bags.

Diseases—Common disease is stem rot caused by *Sclerotinia sclerotiorum* which can be controlled by doing crop sanitation practice and spraying the crop with 1% Bordeaux mixture.

Other diseases of mesta are :—

- (a) Dry rot caused by—*Macrophomina phaseoli*
- (b) Leaf spot caused by—*Cereospora hibisci*

- (c) Leaf blight caused by—*Phyllosticta hibisci*
- (d) Stem rot caused by—*Diplodia hibiscina*
- (e) Anthracnose caused by—*Colletotrichum hibisci*

9.5 *Agave* (*Konga*, *Sisal*, *Sann*) : Fibres obtained from different species of *Agave* are hard and structural fibres. In America, agave fibres stand next to cotton in importance.

The genus *Agave* belongs to the family Agavaceae. All species are perennial shrubs with short rhizomatous woody stems. Leaves large, thick and fleshy, densely crowded on stem apices, margins serrate and spiny. Flowers yellowish green, solitary, fascicled or paniculate on a very long pole-like thick scape reaching a height of several metre. Flowers regular, bisexual. Perianth funnel-shaped, tube short, 6 (3+3). Stamens adnate to the base and longer than perianth segments. Ovary 3-celled, each cell many-ovuled, ovule biseriate. Style more or less long ; stigma 3-lobed. Fruit a leathery loculicidal capsule. Seeds obliquely flattened, testa black.

There are several species of *Agave* which are of commercial importance. In all species, fibres are obtained from leaves. Agave fibres obtained from different species are known by several trade names, these are :—

(1) HENEQUEN or MEXICAN SISAL, obtained from *Agave fourcroydes* Lem.—it is a native of Mexico, now-a-days cultivated in Yucatan and Cuba. In this species, fibre is scraped out from leaf tissue. Fibre is light straw coloured, hard and elastic, measuring from 0.6 m to 1.5 m in length. This fibre is used for binder-twine, lariats etc.

(2) SISAL agave is obtained from *Agave sisalana* Perr. This species is devoid of spines on leaves. It is a native species of Mexico and Central America. In India, it is found in Assam, Bihar, West Bengal, Tamil Nadu, Mysore and Maharashtra.

Fibre of sisal is coarse, stiff, light yellow or white ; it is removed from the leaves either by hand or by the help of a 'raspador'. Fibres are cleaned in water, dried in sun and tied in 271 kg. bales for transport.

Sisal fibre is used in the manufacture of ropes and cords. Sisal wax is used in the manufacture of polishing materials and carbon papers.

(3) MANILA MAGUEY or CANTALA is obtained from *Agave cantala* Roxb.—native of Mexico. In India, it is grown in Punjab, U.P., Bihar, Tamil Nadu and Maharashtra as an introduced type. Fibre, extracted from leaves, is used in the manufacture of cordage, ropes and twines.

(4) ISTLE—Two types are obtained from two different species of *Agave* e.g. jaumave istle from *A. fuukiana* and tula istle from *A. lecheguilla*. Fibres are obtained from immature leaves, they are

extracted by hand ; fibres are stiff, very strong and durable although they are shorter than those of sisal and henequen fibres. Fibres are used in making brushes, bags, twine and rope.

(5) BLUE ELEPHANT ALOE or *Kuwarbuti* is *Agave vera-cruz* Mill. The leaves yield a fibre which is used in making ropes, cordage and mats. This plant is found to grow in S. India.

Climate—Agave plants are xerophytes and exceedingly drought resistant. It grows well in dry and arid regions where the rainfall varies from 100 mm to 200 mm per annum.

Soil—It thrives best in well-lighted and well-drained, dry arid and desert soil which is sandy and clayey loam in nature.

Cultivation, Harvesting, Retting etc.—Plants are generally propagated by means of bulbils or suckers. The land is normally prepared by the help of plough and ladder. First harvesting is done when the plants become 2-3 years old, in this stage leaves are cropped off. After this, fresh harvests are done for a period of 4-6 years. After harvesting, the spines of leaves are removed and the leaves are tied into bundles. Next retting is done in water for several days (6-15 days) and finally the fibres are removed either by hand or machine. Then fibres are thoroughly cleaned in clear water, dried in the sun or in centrifugal machine and tied in bales. The fibre content of dry leaves is about 3-4%.

Diseases—Common disease is Anthracnose caused by *Colletorichum agaves*—it can be controlled by removing and burning affected leaves, and also by spraying crop with 1% Bordeaux mixture.

CHAPTER 10

Timber-yielding Plants and Bamboos

Timber is a term applied to larger sizes of neatly prepared wood of the stem, intended for heavy constructions. Roughly prepared wood of the stem that has been prepared for future use mainly is termed as *lumber*. Wood is the secondary tissue produced by the activity of the cambium in the stems of gymnosperms and dicotyledonous angiosperms. Woods are of two types viz, *sapwood* and *heartwood*—former is a light.coloured outer region of the wood while the latter is a dark-coloured inner region of the wood. Both sapwood and heartwood may constitute timber, but the timber obtained from heartwood is more durable and of good quality.

Timbers are mainly used for making bridges, buildings, beams, posts, joists, planks, railway sleepers, ships, boats, doors and windows, furniture etc. Lumbers are also used in addition to timber in the manufacture of boxes, crates, baskets etc.

10.1 Teak (*Sagun, Singurn*) is obtained from *Tectona grandis* Linn. f. belonging to the family Verbenaceae.

Teak plant is a large deciduous tree. Bark 9.0 mm thick, light brown or grey, fibrous. Wood moderately hard, strongly and characteristically scented—sapwood white, generally small; heartwood dark golden-yellow, turning dark-coloured with age. Annual rings are marked by one or more line of regularly arranged pores; in other parts of wood pores are scattered. Medullary rays are moderately broad to broad. Pith is large, quadrangular.

Trees are stellate-tomentose. Leaves large, petioled, entire, opposite or whorled. Flowers many in dichotomous cymes arranged in terminal panicles. Calyx 5-6 lobed. Petals 5-6, connate. Stamens 5 or 6. Carpels 4. Fruit a 4-celled drupe.

In India, teak is grown in deciduous forests of the peninsular region like Chanda district of M. P., North Kanara : Wynaad, the Anamalai hills and Travancore. In W. Bengal, teak grows in Bamunpokri in the Darjeeling Terai and near Dibrugarh of Assam Valley. Besides India, teak is found in Burma, Siam, Cambodia, Cochin China, Java and Dutch Indies.

Climate—The mean annual temperature required for best growth lies between 22°C and 27°C. Teak grows well throughout the entire season of the year but the temperature requirement varies in different regions.

Soil—Teak grows on various soils such as on sandstone and metamorphic rocks, on laterite, sometimes on limestone, on black

alluvial land etc. For better growth and straight timber, a good drainage system in the soil is required.

Propagation and Cultivation—Teak is propagated from seeds. Seeds are sown in nurseries ; for better and quick germination these should be mixed with sand and dead leaves after being thoroughly soaked. Immediately after germination, young seedlings are planted straight into the forest field. Teak is often found to grow associated with bamboos and other trees over which it forms a kind of upper storey. According to Gamble, teak cultivation may be improved if the following operations are carried out :—“(1) not to girdle isolated trees unless with the object of relieving existing seedlings ; (2) to leave sound trees, likely to improve, in localities whence large timber can be extracted, (3) to fell and not to girdle trees attacked by epiphytic *Ficus*, (4) to continue ‘taungya’¹ plantations with energy and to weed such plantation regularly, (5) to sow or plant up areas of flowered bamboos and (6) to pay much attention to creeper-cutting.”

Uses—Teak is the main building timber of the country. The wood is used for house and ship building, for bridges, railway sleepers, furniture, shingles etc. The wood is very hard and durable—this is due to the large amount of oil contained in the wood.

Insect Pests—Common insect pests are :—Tree borer (*Psiloptera fastuosa*), stem borer (*Cossus cadambe*), teak leaf roller (*Paliga damastesalis*) etc.

10.2 Sal ; *Shorea robusta* Gaertn f. is the botanical name of ‘sal’ tree, it belongs to the family Dipterocarpaceae. Plant is a large gregarious tree. Bark of young trees smooth, with some vertical cracks 2.5-5.0 cm thick in old trees, dark coloured. Wood—sapwood small, whitish ; heartwood brown, pale but later becomes dark on exposure, hard. Annual rings are only visible in young trees on freshly cut wood. Pores are moderate sized to large, often filled with resin. Medullary rays are uniform, moderately broad, straight, prominent.

Leaves entire or sub-repand, coriaceous, stipulate. Flowers in axillary or terminal laxly paniced cymes. Calyx 5-lobed. Petals 5. Stamens 15, 20 or more. Carpels 3. Fruit leathery indehiscent samaroid type, rarely 2-valved, dehiscent, enclosed by winged calyx. Seed solitary.

In India, sal trees grow as forests in two major regions, one at the foot hills of the Himalayas and running into its valleys and up its lower hills to 1,216 m (Dehra Dun, Kumaon, Gorakhpur, Nepal, the Darjeeling Terai, West and East Duars and Assam Valley) and secondly at the Central Indian belt (Rajmahal, Santhal Parganas, Chota nagpur, Madhya Pradesh, Orissa and the northern Circars).

¹ Under this system, “villagers are allowed to cut and burn certain areas of forest and then to cultivate the land, under agreement to hand it over when done with, with so many good teak plants planted per acre, for which plants they receive payment.”

Climate—Sal tree requires variable type of climatic condition for better growth. The rainfall required for germination of seeds, growth of seedlings etc. varies from 103 cm-650 cm per annum. Temperature requirement is also variable.

Soil—The most suitable soil is either sandstone, or alternating beds of shingle and sand or loam (gravelly or sandy).

Propagation and Cultivation—Plants are propagated by seeds under the 'taungya' system. Seeds are sown in well-prepared field in rows with the help of drills. Germination of seeds takes place readily at the commencement of rains. Seedlings spring up very quickly—they are frequently weeded and hoed; watering is very essential at this stage otherwise seedling may die due to dry condition during hot season. The area under the 'sal' cultivation is generally protected against sun and frost by planting other trees or young trees at the edges. Unless sufficient moisture in the soil is retained, the seedlings do not develop into trees having strong and fine shoots.

Mature tree attains a height of 30.5-45.5 m and a girth of 6.0-7.5 m.

Diseases and Insect Pests—Most common and important disease is a sooty black mildew; among insect pests—Cerambycid beetle (*Plocederus obesus*), Sal girdler (*Coelosterna scabrata*), Buprestid beetle (*Chrysobothrys sexnotata*) etc. are important.

Uses—Sal timber is used extensively for various purposes e.g., for piles, beams, planking and railing of bridges; for beams, door and window frames of houses, for gun-carriages; for making railway sleepers and canoes. A type of whitish, aromatic, transparent resin known as 'lal dhuna' is obtained from the tree when tapped—it is used to caulk boats and ships and as incense.

10.3 Mahogany: Mahogany timber is obtained from *Swietenia mahagoni* (Linn.) Jacq. belonging to the family Meliaceae.

Plant is a large evergreen tree. Wood is hard, reddish-brown, seasons well. Annual rings are marked by a continuous line of pores. Pores moderate-sized, scanty, uniformly distributed, sometimes filled with resin. Medullary rays are very short, numerous, moderately broad, uniform and giving a silver-green appearance.

Tree often with buttresses. Leaves even pinnate, leaflets opposite, deciduous, exstipulate. Flowers bisexual, small in axillary and sub-terminal panicles. Calyx 5-fid. Petals 5, spreading. Stamens connate in an urceolate 10-toothed tube. Ovary sessile, 5-chambered. Fruit a 5-chambered capsule.

Mahogany is a native of Jamaica and Central America; in India it is now cultivated in W. Bengal (Darjeeling Terai), northern India (Saharanpur) and at the foot hills of Nilgiris (Nilambur, Kullar).

Mahogany has been found to grow well "near the sea in a moist equable climate" or in a region with a "frosty winter season." Soil

rich in humus arid mould is perhaps most suitable for the natural growth of mahogany. Cultivation on good soil near the sea also gives better growth of plants.

The wood is used mainly for making furniture and cabinet, also used in ship-building.

The most serious insect pest is the Toon borer moth (*Magiria robusta*)

10.4 Sissoo : It is another important timber plant, botanically known as *Dalbergia sissoo* Roxb. belonging to the sub-family Papilionaceae of the family Leguminosae.

Plant is a large-deciduous tree. Bark 12·7 mm thick, grey. Wood very hard, close-grained ; sapwood small, white ; heartwood brown. Annual rings not well-marked. Pores large and moderate sized, scanty, in light-coloured irregular patches which are joined by more or less concentric streaks ; often filled with resin. Medullary rays pale, very fine, uniform, equidistant, numerous.

Large tree, reaching a height of 10·8 m or more, often irregularly buttressed. Leaves odd-pinnate, alternate ; leaflets 3-7, roundish, distinctly cuspidate. Flowers in axillary panicles, small, pedicels short. Stamens 10, monadelphous. Fruit narrow pod.

Sissoo occurs as gregarious in forests of sub-Himalayan tracts and Himalayan valleys up to 914 m from Indus to Assam on the banks of sandy and stony torrential rivers. It is extensively cultivated in Punjab, U. P., West Bengal and Assam. Sissoo is also planted on road sides as shade tree in tea plantations.

Sissoo grows well on porous soils having sand, pebbles and boulders. It reaches its best development on river-bed soils which neither too wet nor water-logged and in all climatic conditions, in association with the species of *Acacia*, *Albizia* and *Salmalia*.

Sissoo is propagated by sowing thin, light and indehiscent pods ; The tree sheds its pods during December-April and seeds germinate at the commencement of rains. Germination of seeds takes place by the decay of the thin outer covering of pods. Seedlings are generally grown in 1·8 m cylindrical tiles, then they are transplanted in pits of the same depth. Full light and weed-free porous soil with sufficient moisture favours the development of seedlings. Irrigation is very essential for better growth of the plant, hence trees are generally planted near the canal. Sissoo also reproduces itself better from suckers and to obtain suckers it is best to cut the tree at a short distance below ground, when numerous suckers appear all round.

The usual method of raising sissoo is stump planting which is widely followed in irrigated plantation in Punjab and U. P. Trenches are dug about 1·5 m apart. About 55 kg. of pods are required for sowing an acre of nursery with sowings done on both sides of the trenches. Sowing is normally carried out between middle of March

and the middle of June. Plants are big enough by the beginning of the next season to yield stumps. The yield of stumps is 40,000 per acre. For transport over long distances, stumps are made into bundles, wrapped in leaves or grasses, sprinkled with water and carried in gunny bags. Spring is the best time for planting stumps. Stumps are planted along trenches or on berms of pits, and the field is irrigated. Depending upon weather and the conditions of the plants, 10-15 irrigations are enough in the first season and 4-6 in the second. Irrigated plantations yield better quality of timber. For raising plantation without irrigation, pod segments are sown directly in lines. The spacing adopted in sissoo planting varies in different areas. A spacing 1.5 m apart in lines 3.0 m in between has proved satisfactory. All sissoo plantations should be thinned out when young and the area sown or planted with other species with only a certain proportion of sissoo trees standing. *Morus alba* is suitable for inter-planting in sissoo plantations.

In irrigated plantations trees reach a girth of 1.2 m 25-30 years ; a height of 9.5 m in 20 months has been reported.

Uses—The wood is very durable, it seasons well. It is extensively used for making boats, carts and carriages, agricultural implements, in construction and specially for furniture.

Diseases—The wood of Sissoo tree is attacked by some parasitic members of bracket fungi like species of *Polyporus*, *Polystictus* etc.

10.5 Pine : Pine is the common English name for several species of *Pinus* belonging to the family Pinaceae of Gymnosperms.

Pine is an evergreen tree and is distributed throughout the tropical to sub-temperate and temperate regions of both old and new worlds.

In India, five species are indigenous, some of these are often cultivated, the chief being cluster or Maritime pine (*Pinus pinaster* Soland). Pines are cultivated both for timber and for resin in the Nilgiris and at various places in Himalayas.

The wood obtained from different species of *Pinus* either belongs to *soft-pine* group (also known as *white pines*) or *hard pine* group (also known as *yellow pines*)—the former has a straight and soft grained wood of uniform consistency while the latter has a resinous, heavy, hard, strong and durable wood.

A. *P. wallichiana* A. B. Jackson (Syn. *P. excelsa* Wall., *P. griffithii* M'Clelt)—This species is commonly known as Indian blue pine or five-leaved pine ; in India it occurs in western and eastern temperate Himalayas at 2,027 to 4,152 m.

A large evergreen tree reaching a height of 30.4 to 36.5 m or even 45.5 m, with a girth of 1.8-3.6 m. Bark greyish brown. Wood moderately hard. Sapwood white, heartwood light red. Annual rings are marked by denser autumn wood with compressed tracheids and

smaller lumina. Medullary rays are fine, more or less irregular. Resin ducts scattered, prominent on all sections.

Needles are large, 5-8 in a cluster ; cones are larger, cylindrical and soft-scaled.

Indian blue pine thrives well at high elevation in a cold climate having an annual rainfall varying from 30.5 cm to 485.5 cm. ; for better growth, it prefers sandy or clayey soils rather than limestone.

Blue pine is propagated from seeds. If grown in pure forests, it can be treated "by a heavy seed-felling and breaking up of the soil, to be followed by a final felling when the seedlings have come up and are strong enough." For better transplanting, seedlings should be placed in baskets at an early stage and used the baskets in planting. Blue pine is found either gregarious or mixed with other trees such as Deodar.

Uses—The timber obtained from blue pine is very good. It is largely used in the construction of planking, doors, window, furniture, pencils, match and tea boxes etc. Resinous wood is also used for torches.

Diseases and Insect Pests—Most serious funguous disease is caused by *Peridermium orientale* which occurs as little orange-coloured sacs of spores on the needles of the trees. Among insect pests, small beetles of the genus *Polygraphus* cause the destruction of the bark and outer sapwood.

B. *P. roxburghii* Sar. (Syn. *P. longifolia* Roxb.). This species is known as long-leaved or three-leaved pine. In India, it is found to occur in outer Himalayas and Siwalik range, also in the valleys of Himalayan rivers at 457.0 to 2,133.6 m—extending West to N.W.F.A. and East to Bhutan.

A large more or less deciduous tree. Bark reddish-brown outside, dark-red within. Wood moderately hard ; sapwood white, heartwood light reddish-brown. Annual rings are very distinct. Medullary rays are fine, rather irregular. Resin ducts large, numerous, prominent in longitudinal sections. Needles are long (21.5-25.5 cm) in clusters of 3. Cones are large and woody.

Long-leaved pine grows in varying forest-soil and climate. It is propagated from seeds wherever the forest is protected from fire. Before propagation, the thick carpet of grass and dry needles should be removed from the ground. In treatment it resembles the Scotch pine and the best method is to make a heavy seed-felling, leaving only a few well-spaced good seed-givers and to stir up the soil. The long-leaved pine may be grown easily in nursery but direct sowings have been found to be more satisfactory than planting seedlings. If transplanting is necessary, it should be done in winter or in summer rather than in monsoon as the tree can not tolerate wet and water-logged condition of the soil.

Uses—The wood is used for construction work, railway sleepers, packing cases, furniture and in match industry. The rosin or colophony is mainly used for soap manufacture.

Diseases and Insect Pests—The fungous disease is same like that of Indian blue pine. Among insect pests the attack of Curculionid beetle (*Astycus lateralis*) and small grasshoppers (*Caloptenus*, *Catantops* etc.) are serious.

Other common Indian species are :—

1. *P. insularis* Endl. (Syn. *P. khasya* Royle ex Parl.)

This species is known as Khasi pine or Benguet pine—found to grow in eastern Himalayas, specially in the Khasia and Jaintia hills.

It is a large evergreen tree reaching a height up to 60.5 m with a girth of 3.0 m. or more. Bark thick, with deep cracks. Wood very resinous, pale-brown to red. Annual rings are distinct ; numerous, moderate sized.

The wood is extensively used in the Khasia hills for building and other purposes. Wood is very rich in resin which is used in making turpentine and varnishes.

2. *P. gerardiana* Wall.—Commonly known as Himalayan edible pine or Neosia pine, found to grow in dry and arid West Himalayas between 1,128 and 3,040 m altitudes.

A moderate sized evergreen tree. Bark is very thin, smooth, grey in colour. Wood is hard and resinous, heartwood yellowish-brown. Annual rings are distinct. Medullary rays are fine but not prominent. Resin ducts are scattered and moderately large.

The oily seeds form a staple food in Kunawar and other parts of the Himalaya. The wood is used for 'hook', the bark is made into baskets and rough water-buckets.

10.6 Bamboos (*Bans*) : Bamboos are all tall arborescent grass belonging to the tribe Bambuseae of the family Gramineae. Bamboos are found to grow in humid tropical and extra-tropical regions of Eastern Asia and South America.

In India about 136 species of bamboos occur, of which the common and important ones are :—(i) *Bambusa bambos* (L.) Willd. (spiny bamboo or '*Bans*'—found to grow throughout the plains and low hills of Assam, W. Bengal, southern and western India) ; (ii) *B. vulgaris* Schrader (feathery bamboo or '*Basini bans*'—found both in plains and hills of Assam and W. Bengal) ; (iii) *B. tulda* Roxb. (*Tulda* or '*Paka-bans*'—found to grow in Assam, Bihar, Orissa and W. Bengal) ; (iv) *B. balcooa* Roxb. (plaini bamboo or '*Balka-bans*'—found in Assam, Bihar, Orissa and W. Bengal) ; (v) *B. nana* Roxb. ('*Chota bans*'—found to grow in gardens of W. Bengal) ; (vi) *Bambusa polymorpha* Munro ('*Betua-bans*'—growing in Assam and W. Bengal) ; (vii) *Thamnocalamus aristatus* Camus (Syn. *Arundinacea aristata* Gamb.—found in Eastern Himalayas) ; (viii) *Pseudostachyum polymorphum* Munro. (growing in the valleys of Eastern Himalayas, Assam and Sikkim) ; (ix) *Dendrocalamus strictus* Nees (Solid bamboo or '*Bans-kaban*'—found to grow in deciduous forests throughout India) etc.

Besides India, other bamboo growing countries are Ceylon, Burma, Bangladesh, Pakistan, Malayasia, Indonesia, Philippines, Australia, China, West Indies, South America etc.

Bamboos are perennial, evergreen or deciduous trees or shrubs. Stems are woody and jointed—commonly called ‘culms’ arising from woody rhizomes. The culms are normally round and glabrous, greenish or yellowish in colour, hollow at internodes but provided with transverse septa at nodes. The diameter of stem ranges from 0.3 m. to 4.5 m. Leaves are $\frac{1}{2}$ alternate, lanceolate, ligulate; lamina many-nerved with petiole-like base articulate with the sheath. Spikelets ovate, bisexual, many-flowered usually. Flowers are green and inconspicuous. Glumes ovate-mucronate, spinescent, many-nerved. Lemmas awnless. Lodicules 3 or absent. Stamens 6 or more. Styles simple or bifid. Stigmas 2-3. Ovary hairy above, often depressed. Fruit caryopsis or small nut with coriaceous or crustaceous pericarp. Seeds are usually grains.

Climate—Bamboos grow best in moist and humid climate i.e. in the well-drained parts of the monsoon forest region at the foot hills of Himalayas.

Soil—Moist and well-drained clayey or loamy soil is most suitable for the cultivation of bamboos.

Cultivation—Bamboos are generally propagated by offsets, cuttings and by layering. In case of virgin land, clearance of scrub growth is essential. Pits 12-14 cubits apart should be dug two or three months before sowing. The soil may be manured with oil-cakes, tank earth etc. Next offsets or cuttings are planted in pits in the rainy season during the months of May to July. The bamboo tree attains maturity within 8-12 months, after which they are harvested by cutting from the ground and sent to the market.

Uses—Bamboos are used in place of timbers in the construction of houses. They are also used in making ladders, bridges, fences, supports, tent-poles, yokes etc. Some useful articles such as tool-handles, stick, cordage, beds, brushes, pipes, umbrellas, toys, bows and arrows, baskets, furniture, mats, chiks etc. are also made from different types of bamboo splits. Now-a-days, bamboos are used in the large scale manufacture of paper in India. The young shoots of *Bambusa tulda* are often used as a vegetable.

Diseases and Insect Pests—Bamboos are often found to suffer from fungal diseases by some members of Basidiomycetes—these are *Portia diversipora*, *Guepinia spathularia*, *Daedalea flavida*, *Polyporus durus* etc. Control measures are not yet known.

Among insect pests, borer beetles (*Dinoderus* spp., *Sinoxylon* and *Lyctus* spp.) are main—all these may be controlled by injecting some preservatives (a mixture of creosote and fuel-oil in the proportion 1 : 1) at internodes—superficial swabbing of culms with preservatives also gives temporary protection.

Rubber-yielding Plants

Rubber is a tough elastic substance obtained from the latex of several woody plants of the tropics and sub-tropics. Most of the rubber plants belong to the families Euphorbiaceae, Moraceae and Apocynaceae. Latex is a gummy and white or yellowish-white colloidal secretion ; it is a mixture of several substances like water, hydrocarbons, proteins, sugar, salts, oils, resins, acids and caoutchouc—the last one is mainly used as the source of rubber. Latex occurs in laticiferous cells or vessels present in various plant parts.

The word ‘rubber’ is named from rubbing out pencil marks and was first applied by Priestley in 1770. This property of erasing or removing of pencil marks is due to the presence of caoutchouc in the latex of rubber plants. Other properties of rubber are its resistance to electrical currents, impermeability to liquids and gases, plasticity and elasticity. The coagulated latex in rubber contains a high percentage of a highly elastic polymercis-polyisoprene.

The use of rubber is various now-a-days ; it is much used in the manufacture of tyres and tubes, shoes, balls, water-proof clothings, various electrical and surgical goods and many other purposes.

11.1 Hevea or Para-rubber (*Rabar*, *Ruber*) : Para-rubber is obtained from the plant *Hevea brasiliensis* (H. B. & K.) Muell-Arg. belonging to the family Euphorbiaceae. This plant is the source of 98 to 99% natural rubber produced in the world. *Hevea brasiliensis* was first cultivated as rubber plant in the Para district of Brazil, hence it is named para-rubber. From Brazil the plant was introduced to India and Sri Lanka (Ceylon) in 1876 by Sir Henry Wickham through Kew Botanic Garden.

Para-rubber is cultivated extensively in India, Ceylon, Malayasia and Indonesia. In India, it is grown in Kerala, Tamil-Nadu, Mysore (Karnatak) and North-East Assam. At present about 3·5 lakh acres are under the cultivation of this crop in India.

Hevea brasiliensis is a native of Brazil. Plant is a hardy, tall and branched tree, reaching 10-30·5 m or more in height. Branches are spreading forming a canopy. Mature leaves are dark green, alternate, compound with three leaflets. Flowers are produced in axillary panicles at the end of the branches. Flowers are small, unisexual, monoecious and sweet-smelling ; female flowers are larger than male, situated at the distal ends of the branches of panicles. Fruits are 3-seeded capsules. Seeds with hard testa and oily endosperm.

Climate—A uniform climate with a temperature range of 23·8°C to 35°C, a well-distributed rainfall of 180 cm per annum and high atmospheric humidity favours the cultivation of para-rubber plant.

Soil—Para-rubber plant grows best on deep, well-drained loamy soils of 4.5 to 6 pH.

Cultivation—Plants are propagated either from selected seeds or from buds vegetatively. In the former case, seeds are allowed to germinate in beds made of river sand; then germinated seeds are planted in specially prepared nursery beds about 0.6 m wide and of suitable lengths.

The soil in the nursery bed should be well-ploughed, pulverised and mixed with fertilizers. When the seedlings attain a height of 0.5 m and a diameter of 19.0 mm-25.5 mm above the collar they are transplanted during June-July in prepared pits in the field with spacing 4.5 m \times 3.0 m or 6.0 m \times 6.0 m.

Vegetative propagation by buddings from mother clones may be done. Budded stocks are cut 10.0-15.0 cm above the bud patch and then they are transplanted in the field with a spacing 4.8 m \times 4.8 m or 6.6m \times 3.3 m.

Some leguminous crops are raised between the trees as cover crop to prevent soil erosion, to maintain soil moisture, low temperature of soil and also to add humus and nitrogen to the soil. Application of fertilizer mixtures of N,P,K (1 : 1.5 : 1.5) at the rate of 0.42 kg. for each year of growth with a maximum of 1.6 kg. per plant per annum from the 5th year onwards is necessary.

Tapping—It is the process by means of which the bark is cut to induce the flow of latex. Three to four years old trees are tapped in the early morning. Bark is cut by mallet and chisel in the form of a half spiral i.e. first vertically at a slight angle to the right and extending down to the right. Tapping should be deep enough so as to reach near the cambium. At the base of the cut groove, an iron or zinc spout is placed; spout leads into a half coconut shell fixed in various ways in which the latex is collected. For seedling trees, tapping should be once in three days while for budded trees it should be done on alternate days. Tapping is continued almost throughout the year except during monsoon and wintering periods, when it is suspended for 4-6 weeks. After the latex has been collected, anti-coagulant is sometimes added to the collecting vessel to keep it liquid until the latex is taken to the factory for processing.

Yield—In India, the average yield of dry rubber per acre per annum varies from 90.5 kg. to 670.5 kg.

Processing—Latex contains about 33% of dry rubber. Immediately after reaching the factory, latex is passed through sieves to remove impurities; then pure latex is mixed with water, allowed to stand and again passed through sieves. Then the entire content is poured into aluminium trays of standard size to which suitable quantity of formic or acetic acid of required strength is added to coagulate and stirred. The coagulated rubber is a soft whitish mass which is washed in running water and then passed between smooth rollers to squeeze out water—in this operation the coagulated rubber mass is converted

into sheets. Next, sheets are again rolled in grooved roller. Then sheets are dried partially in open air and finally in smoke houses for thorough drying at a temperature of 49°C-62°C. After this, sheets are graded according to quality and packed for despatch to the market. In India, the average annual production of natural rubber is 30,000 metric tonnes.

Uses—In the modern world rubber is used in the manufacture of about 50,000 different products either directly or indirectly. It has been estimated that about 6% of the total world production is used in footwear industry viz shoes, boots, soles, heels etc. and about 4% in insulation of cables and wires. Rubber is also used extensively in the manufacture of sports goods, transmission and conveyor beltings, shock absorbers, gaskets and washers, hosepipes, tyres and tubes in automobile industry, rubberised fabrics and various household products, foamed rubber in upholstery and mattresses; ebonite or vulcanite (hard, sulphurised rubber) in radio and electrical industries and in chemical plants as lining etc. etc.

Varieties—Most of the high-yielding varieties in India are introduced from countries like Java, Malaya, Sumatra and Ceylon. Such varieties are named after the experimental stations or plantations from where they have originated. Following are the names of several high-yielding varieties of Para-rubber :—

1. RRIM, Prang Basar, Glenshiel - introduced from Ceylon
2. Tirandji, Dater, Bodjong -- " Java
3. AVROS-Algemene; Verneiging Rubber
Planters Oostkut— " Sumatra
4. Millikande, Wagga, Hillcroft— " Ceylon

Besides the above mentioned varieties, other two important varieties grown to a considerable extent are Tjir I and Prang Basar Isolated Gardens.

Diseases and Insect Pests—Common diseases are—(1) Abnormal leaf fall, Black thread, Canker and Pod rot caused by *Phytophthora palmivora* - it can be controlled by treating the tapping surface with Albolinum solution and spraying oil based copper oxychloride @ 0.8 kg. copper to 9 litres oil per acre. (2) Dieback caused by *Botryodiplodia theobromae*, control by pruning diseased parts, (3) Bird's eye spot caused by *Helminthosporium heveae*—control by spraying the crop with 0.5% Bordeaux mixture. (4) Powdery mildew caused by *Oidium heveae*—it can be controlled by dusting crop with sulphur @ 3.5 kg. per acre. Other diseases of Rubber tree include, (a) South American leaf blight (*Dothidella ulei*)—growing resistant clones is the best method of control; (b) Mouldy rot (*Ceratocystis fimbriata*)—may be controlled by reducing intensity of tapping and applying fungicides.

Common insect pest is Para-Rubber Termite (*Ghyptotermes dilatatus*)—it can be controlled by adding 5% Aldrin dust in the soil around the trees.

SOME OTHER IMPORTANT RUBBER-YIELDING PLANTS

11.2 Assam Rubber or India Rubber : It is obtained from the plant *Ficus elastica* Roxb. belonging to the family Moraceae. It is a native of India and Malaya. In India, this plant grows in Assam and Khasia hills.

Ficus elastica is a giant tree with buttresses and prop roots. It grows well in hot climate where annual rainfall is very high.

The tree requires 40-50 years to mature for better yield. Both prop roots and stems are tapped. The latex is collected on bamboo mats where it coagulates. The yield of this rubber is very low, about 200-500 grams per tree per annum. Assam rubber is also of low grade, hence it has little or no commercial importance.

11.3 Ceara or Manicoba Rubber : It is obtained from the plant *Manihot glaziovii* Muell-Arg. belonging to the family Euphorbiaceae. It is a native of Brazil, it is also grown in India, Ceylon and other tropical countries.

Manihot glaziovii is a tall tree reaching a height of 9-10 m.

Plants 4-5 years old are generally tapped. Latex is obtained from the stem and roots of the plant, it yields a good grade of rubber. The latex is coagulated by exposure to smoke or air.

11.4 Panama or Castilla Rubber : It is obtained from *Castilloa elastica* Cerv. belonging to the family Moraceae. It is a native of Mexico and Central America.

Plant is a tall tree reaching a height up to 45 m. It grows only in deep loamy soils on high land.

Plants 8-10 years old are tapped, latex is obtained from the stem mainly and in the same manner like that of Hevea rubber. Adult tree yields up to 22.5 kg. of latex per annum. The latex is coagulated with plant juices or alum and by boiling or exposure to air.

Oils are chemical compounds of carbon, hydrogen and oxygen (but the ratio of hydrogen to oxygen is not 2 : 1) which remain liquid at ordinary temperature (10°C-20°C). The solid state of oils is termed as fats. Oils obtained from the various parts of plants fall under two main categories viz. (a) *essential* or *volatile oils* and (b) *fatty* or *fixed oils*. Essential oils are highly aromatic substances, mostly benzene or terpene derivatives or straight-chain hydrocarbon compounds of intermediate molecular length; they evaporate or volatilize in contact with air and are extracted by distillation or by solvents mainly. Fatty oils do not evaporate or volatilize and they can not be extracted by simple distillation method.

Fatty oils are composed of glycerin together with fatty acid, these are stored up in many plant parts like seeds, fruits and other organs. Fatty oils are produced by large number of both tropical and temperate plants.

Fatty oils are of four types viz. (a) *drying oils* which form thin elastic film on exposure to air e.g. linseed oil, niger-seed oil, soyabean oil etc.; (b) *semi-drying oils* which form a soft film on exposure to air e.g. cotton-seed oil; (c) *non-drying oils*, this never form a film but remain liquid at ordinary temperature e.g. mustard oil, castor oil, groundnut oil, olive oil etc. and (d) *fats* or *tallows* that remain solid or semi-solid at ordinary temperature e.g. coconut oil, mohua oil etc.

12.1 Linseed oil : (*Tishi*, *Alsi*) : It is obtained from the flax plant *Linum usitatissimum* L. of the family Linaceae. In India, flax plant is grown mainly for the oil contained in the seed while in western countries it is grown mainly for the fibre obtained from the stem and used in the manufacture of linen (refer art. 9.3).

Besides India, other major linseed oil growing countries are USA, Canada, Argentina, Uruguay, China and USSR. In India, the crop is chiefly cultivated in Madhya Pradesh, U. P., Maharashtra, Bihar and Rajasthan. India occupies the fifth rank among the linseed producing countries of the world and about 4.3 million acres of lands are in cultivation with an average annual production of 3.9 lakh tonnes.

Linum usitatissimum is a slender annual herb. For botanical description of the plant see art. 9.3, para 5.

Climate—Linseed for oil grows well in moderate cold climate and in areas with annual rainfall ranging from 45.5 cm to 75.9 cm. It can be cultivated in plains as well as in hills up to an elevation of 7,60 metre.

Soil—Linseed can be grown on variety of soils but the best soils for its cultivation are clay loams, alluvium loams and deep clayey black soils.

Cultivation—In India linseed is grown in *rabi* season from September-October to February-March. The land should be ploughed and harrowed several times so that a clean well-pulverised but firm seed bed may be obtained. Seed is sown in October at the rate of 4.5-6.7 kg. (for small seeded type) or 9.0-11.0 kg. (for bold seeded type) per acre with a *mogha*, or 3 or 4 coultured drill in rows 20.0-30.0 cm apart and then covered by a light harrow. Seeds are also sown broadcast in some tracts. Interculturing or manuring is not essential when the crop is grown alone. For better yield, 6.7-18.0 kg. nitrogen per acre is recommended.

Harvesting—Depending on the variety grown and the time of sowing the crop begins to mature from the end of January to the end of April. Just at the ripening stage of fruits, the crop is harvested either by cutting them close to the ground or pulling out the plants. Plants are then left for drying in the threshing yard and seeds are finally taken out by beating the plants with sticks or by treading under the feet of cattle. Harvested seeds are stored in various containers for several months. The oil is finally extracted from seeds either by pressure with heat or by *ghanis*.

Yield—The average yield of seeds varies from 67.9-226.5 kg. per acre. The oil content of seeds is 33-43%. The colour of the oil varies from yellow to brownish.

Uses—Linseed oil is mainly used as drying oils in the preparation of paints, varnishes, printing ink, water-proof fabrics and oil-cloth. In India, it is also used as edible oil in some States.

Varieties—The improved varieties recommended for cultivation in different States of India are :

W. Bengal—B 37, B 67 etc.

Bihar—Linseed Teesi ; P 142 ; BR 1, 2, 12 etc.

Maharashtra—Malsiras 10, Sholapur 36, No. 3, No. 55

Madhya Pradesh—No. 3, No. 55, No. 4/29, N.P. 11

Orissa—Mayurbhanj

Uttar Pradesh—Type no 1, Type no 126 etc.

Diseases and Insect Pests—See article 9.3

12.2 Castor oil (*Rehri*) : It is obtained from the seeds of the plant *Ricinus communis* L. of the family Euphorbiaceae.

The plant is chiefly grown for seeds. Besides India, castor is grown in Brazil, Mexico, Egypt, Sudan, China and Manchuria. In India the plant is extensively cultivated in Andhra Pradesh, Maharashtra and Mysore.

Ricinus communis is a native of tropical America. Plant is a tall evergreen, glabrous, annual shrubby or tree like. Leaves alternate, palmately lobed, broad, serrate. Flowers unisexual, large in terminal,

sub-paniculate racemes—male flowers are crowded towards the distal part while female towards the proximal part of the inflorescence axis. Sepals in male flower connate into 3-5 valvate segments, in female flower sepals connate in a spatulate caducous calyx. Stamens numerous, polyadelphous. Carpels 3, connate in a 3-celled ovary. Fruit a capsule of 2-valved cocci, seeds oblong, testa crustaceous, carunculate, albuminous.

Climate—Castor grows well in warm and dry climate having a well-distributed rainfall of 50.5 cm to 75.9 cm per annum.

Soil—The most suitable soils for castor cultivation are red sandy loam and light alluvial soil.

Rotation—Castor may be grown alone or in rotation with cotton, jowar, bajra, groundnut, gram etc.

Cultivation—The crop is raised mainly as a rainfed annual crop but sometimes also as an irrigated crop. The land is ploughed and harrowed twice or thrice. Seed is sown in June-July at the rate of 2.25-4.5 kg. per acre either by dibbling or dropping in furrows with coultered drill. The rows are 0.9-1.5 m apart. The crop is thinned in such a way that one plant stands in a row at a distance of 60-90 cm. One or two weedings and hoeings are given, generally no manuring is done.

Harvesting—The crop matures within six months. The ripe fruits are collected and stacked—it is then dried in the sun for a few days and seeds from fruits are beaten out with mallets or sticks; then they are winnowed. Oil is extracted from seeds by expression in power expellers or in village *ghanis*.

Yield—The average yield of rainfed crop per acre varies from 90.5-226.5 kg. and of irrigated crop from 225.5-262 kg. The oil content of the seed is 50%. Castor oil is very thick, either colourless or greenish in colour.

Uses—Castor oil is mainly used for medicinal (as a purgative), lighting, lubricating and industrial purposes such as in the manufacture of hair-oil, soap, textile-soap, typewriter inks, plastics, varnishes, paints, and as protective coverings for insulation, fabrics, guns, food containers etc.

Varieties—The main improved varieties recommended for cultivation in different States of India are :—

W. Bengal—W. B. 1

Bihar—E. B. 16, T.M.V.-3

Gujrat—N. 20, T.M.V.-2

Tamil Nadu—T.M.V.-3, Co. 1

Maharashtra—Castor 20, E.B. 31

Mysore—Rosy, M.C. 1

Madhya Pradesh—E.B. 9, E.B. 16, E.B. 31

Uttar Pradesh—Tarai 4, Type 3

Diseases and Insect Pests—Common diseases are—(1) Seedling blight and Alternaria blight caused by *Phytophthora parasitica* and *Alternaria ricini* respectively—former may be controlled by avoiding the cultivation of the crop in damp and lowlying areas and the latter by treating seeds with fungicides. (2) Leaf spot caused by *Cercospora ricinella*—it can be controlled by growing resistant varieties.

Common insect pests are :—(1) Castor semilooper (*Achoea janata*)—it can be controlled by spraying plants with lead arsenate or 0.16% DDT or 0.3% Endrin @ 425—636 litres per acre. (2) Castor butterfly (*Ergolis merione*)—it can be controlled by spraying crops with 0.1–0.2% DDT or BHC @ 425—637 litres per acre.

12.3 Groundnut or Peanut oil (*Cheena badam, Mungphali*) : It is obtained from the seeds of the plant *Arachis hypogaea* L. belonging to the sub-family Papilionaceae of the family Leguminosae.

The plant is a native of Brazil from where it was introduced into Asia and Africa in the early part of the 16th Century. India occupies first position in groundnut cultivation. It is extensively cultivated in various States of India like Gujrat, Maharashtra, Andhra Pradesh, Tamil Nadu and Mysore. The average annual area under the cultivation of groundnut in India is 15.4 million acres and the average production is 4.3 million tonnes. Besides India, other groundnut producing countries of the world are USA, West Africa, Nigeria, China, France, Japan and Australia.

Arachis hypogaea is a prostrate much branched annual herb. Leaves are pinnate compound, stipulate. Roots are of both tap and adventitious types. Flowers in dense axillary spikes, sessile or shortly pediceled—generally two types of flowers e.g. sterile and fertile types are developed. Former is with yellow-coloured papilionaceous corolla and latter is without corolla. Stamens 10. Carpel one, ovary sessile, 2-3 ovuled, style long and filiform. Fruit a thick, oblong, reticulate lomentum, *burying itself to ripen underground*. Seeds 1-3, irregularly ovoid ; cotyledons thick, fleshy.

Climate—Groundnut may be cultivated both in tropical and sub-tropical climates and up to an elevation of about 1,060 metre. The plant cannot tolerate frost, continuous drought and water-logged condition. Groundnut grows successfully in areas having an annual rainfall ranging between 50.5 cm-126.5 cm.

Soil—The crop grows best in loam, sandy loam and well-drained black soils.

Rotation—Groundnut may be grown alone or in rotation with wheat, jowar, bajra, paddy, cotton and also with garden crops. It is also cultivated as an inter-crop with castor, cotton, millets etc.

Cultivation—Groundnut is mainly cultivated as rainfed *kharif* crop. To obtain a fine and friable seed bed, the land should be ploughed deeply, followed by harrowings in summer and immediately after the first showers. As a rainfed crop, seeds are sown from April-May or June-July ; but as an irrigated crop seeds are sown between January-March and May-July.

Normally, manuring is not necessary. But in some parts of Mysore and Punjab, the crop is manured with 9-12.0 kg. each of N and P_2O_5 per acre.

Only well-formed seeds i.e. kernels from healthy pods are dibbled by means of hand at 15-22.8 cm. intervals in 7.5-9.0 cm deep furrows behind wooden ploughs. Seeds may also be sown with drills in rows 22.8-30.4 cm apart and then covered with a light harrow. According to variety, seed rate per acre varies from 23.5 kg. (for spreading type) to 45.3 kg. (for bunch type).

One hand weeding and one or two hoeings are given to the crops after sowing—first hoeing should be given about three weeks after sowing while the second about a fortnight later.

Harvesting and Yield—The crop is harvested when the basal leaves of the plant turn yellow and start shedding of leaves. The bunch variety is harvested by pulling out the entire plant by hand while the spreading variety is harvested by digging the soil. Then pods are immediately stripped from the harvested plants, dried in the sun and finally stored as unshelled nuts—they are then despatched to the market.*

The average yield of unshelled pods of spreading variety is 543.5-640 kg. per acre while that of bunch variety 362.4-453 kg. per acre. The average yield of seeds i.e. kernel by pods varies from 70.75% by weight. The oil content of the seed varies from 44-50%.

Uses—Groundnut oil is extensively used for cooking purposes and also in the manufacture of hydrogenated *vanaspati*, margarine, soap and toilet products. The seeds are also used for roasting or salting and for the preparation of peanut butter. Seeds are rich in vitamin A, B and proteins—the calorific value is 349 per 100 gms. The oil-cake is used as a fertilizer and as a cattle feed.

Varieties—Followings are the important and recommended varieties for cultivation in different States of India :—

W. Bengal—AH. 25, B-30, B-31, J-11, Pollachi 1

Bihar—Big Japan, Spanish peanut, AK. 12-24, TMV. 1

Andhra Pradesh—TMV 2, TMV 3, Spanish peanut 5

Madhya Pradesh—AK. 10, AK. 12-24, Improved Small Japan, Improved Spanish

Tamil Nadu—TMV 1, 2, 3, 4

Maharashtra—Spanish improved, Kopergaon 1, Kopergaon 3, Spanish peanut 5, AK. 10, AK. 12-24, Faizpur 1-5, Karad 4-11 etc.

Mysore—HG 1, HG. 7, HG. 9, Pondicherry 8, Spanish improved.

Uttar Pradesh—Type 25, Type 28, Type 100

Rajasthan—R.S. 1

Diseases and Insect Pests—Common diseases are :—(1) Tikka disease caused by *Mycosphaerella personata*—it can be controlled by spraying the crop with 1% Bordeaux mixture or dusting with sulphur. (2) Rosette and mosaic diseases due to virus—control measure is not yet known. (3) Collar rot caused by *Pellicularia rolfsii*—can be controlled by disinfecting soil with chloropicrin and growing resistant varieties. (4) Irregular leaf spot caused by *Mycosphaerella*

arachidicola—control by crop rotation, growing resistant varieties and by spraying with 1% Bordeaux mixture.

Common insect pests are :—Aphids (*Aphis laburni*) and Red hairy caterpillar (*Amsacta albistriga*)—they can be controlled by dusting with 10% BHC or Endrin at 0.012% concentration in the early stage. Dusting of Toxaphene and spraying Folidol or Endrin also give good result. Stem borer (*Sphenoptera perroteti*) is another important insect pest, it can be controlled by removing and destroying infested plants.

12.4 Mustard oil : Mustard oil is obtained from several varieties of oil seeds known as *rape seed* and *mustard* belonging to the genus *Brassica* under the family Cruciferae. These seeds fall under following groups viz. (a) Brown sarson (*Sarisha*, *Sarsoon*) obtained from *Brassica campestris* L. var. *dichotoma* Watt; (b) Yellow sarson or Indian colza (*Sarisha*, *Sarsoon*) obtained from *Brassica campestris* L. var. *sarson* Prain; (c) Indian rape (*Tori sarisha*, *Toria*), obtained from *Brassica campestris* L. var. *toria* Duth. (d) Indian mustard (*Rai*) obtained from *Brassica juncea* (L.) Czern. & Coss. (e) Black mustard (*Benarasi rai*, *Kalisarson*), obtained from *Brassica nigra* Koch. (f) White mustard (*Swet rai*), obtained from *Brassica alba*, *B. hirta* Moench. etc.

Mustard oil crop is cultivated both in tropical and sub-tropical regions of India. In India, the main crop producing States are U.P., Punjab, Bihar, Madhya Pradesh, Orissa, West Bengal and Assam. The average annual area under the cultivation of this crop is 7.5 million acres and the production about 1.4 million tonnes. India occupies the first position in the production of mustard and rape seed in the world. Besides India, mustard oil crop is grown in Bangladesh, China and Pakistan; it is also cultivated in USSR and Europe but the rape seed and mustard growing there differ from those of Indian varieties.

Mustard plant is an annual or biennial herb. Leaves large, lyrate. Inflorescence raceme. Flowers are yellow or white, sepals erect or spreading; petals distinctly clawed. Stamens 6, tetradynamous. Carpels 2. Fruit capsule, elongate, terete or angular. Seeds globose.

Climate—Mustard and rape seed crops require cool weather for better growth. They are grown both in tropical and temperate regions of India, mainly in the *rabi* season.

Soil—Mustard crop grows best both in light and heavy loam soils.

Rotation—It is generally grown mixed with other *rabi* crops. Sometimes rape seed and mustard crops are grown pure—then these crops follow early maize, paddy or legumes.

Cultivation—The land should be ploughed 4-6 times to obtain a fine tilth. In case of mixed cropping, the seeds are sown from September-October to February-March, either in parallel rows 10-15 cm apart alternating with the main crop or broadcast on the entire field at the rate of 0.63-0.84 kg. per acre. For pure crop, seed rate varies from 1.6-2.6 kg. per acre. Spacing between lines, plants and rows varies according to varieties grown—for brown or kali sarson,

toria and rai, a spacing of 45.0 cm between lines and 10-15 cm between plants is followed while in case of yellow sarson, 30.0 cm spacing between rows and 10-15 cm between plants is given. To obtain a better yield, application of nitrogenous fertilizer at the rate of 13.5 kg. for toria, 18-22.6 kg. for sarson and 22.6-27.0 kg. for rai is recommended. One or two irrigations give beneficial effect to some varieties. About a fortnight after sowing, the crop is thinned, weeded and hoed twice.

Harvesting, Threshing, Yield etc.—Crop is harvested when they begin to turn yellow. Plants are harvested by means of hand sickles. After harvesting, they are threshed by beating the fruit bearing part of the plants with the help of a wooden stick or under the feet of cattle. Then seeds are winnowed and finally dried in the sun.

Next, seeds are stored in various containers like gunny bags, seed bins etc. The average yield of rape seed and mustard per acre varies from 155.5 kg. to 542.5 kg. The oil is extracted from seeds by expression in mills or *ghanis* in villages. The oil content of the seeds of different varieties varies from 30-48%. The oil is golden yellow in colour.

Uses—Mustard and rape seed oil is mainly used as edible oil for cooking, it is also used as an illuminant. The seeds are used as condiment in the preparation of curries and vegetables. The oil-cake is used as a cattle feed and as a manure.

Varieties :—The main improved varieties recommended for cultivation in different States of India are as follows :—

(1) W. Bengal—B. 54, T-59 (*Brassica campestris* var. *toria*), B. 85 (*B. juncea*), B-65 (*B. campestris* var. *dichotoma*) and Rai-9 (*B. alba*), Appressed mutant.

(2) Uttar Pradesh—Type 151 and Type 10 (*B. campestris* var. *sarson*), Type I, Type 42, RT I (*B. juncea*), T. 16, Laha 101

(3) Bihar—Br. 23, Br. 29, Br. 32, Br. 36 (all are *B. campestris* var. *toria*); Br. 13, Br. 40 (both are *B. juncea*)

(4) Punjab—Sel. A (*B. campestris* var. *toria*), Faridkot selection (*B. juncea*)

(5) Assam—M-3 (*B. campestris* var. *sarson*), M-18 (*dichotoma*), M-27

Diseases and Insect Pests—Common diseases are—(1) Alternaria blight caused by *Alternaria brassicae*—it can be controlled by growing resistant varieties, and also by treating seeds with hot water (50°C for 10 m's.) and by spraying seed plots with 1% Bordeaux mixture at the seedling stage. Practice of crop rotation is also recommended. (2) White rust caused by *Albugo candida*—it can be controlled by removing and burning affected plant parts.

Common insect pests are—(1) Mustard aphid (*Lipaphis erysimi*)—control measures are clean cultivation and spray the crop with 0.05% nicotine or fish-oil rosin soap or 0.2% BHC @ 318-425 litres per acre. (2) Mustard saw-fly (*Athalia proxima*)—can be controlled by removing larvae and dusting the crop with 3% BHC @ 4.5-9.0 kg. per acre or spraying with 0.1% DDT or BHC @ 318-425 litres per acre.

12.5 Coconut oil (Narikel, Narial or Gola) : This oil is obtained from the dried meat¹ or copra of the coconut plant *Cocos nucifera* L. of the family Palmae.

¹ White cartilage-like kernel

The coconut is cultivated extensively in the saline islands of tropical seas, specially in the humid coastal belts of tropical countries like Bangladesh, India, Ceylon, Polynesia, the Philippine islands and the West Indies. In India, about 1.6 million acres are under coconut cultivation and the average annual production of nuts is 4,375 million. In India, coconut is mainly cultivated in Kerala, Mysore, Tamil Nadu and W. Bengal.

Cocos nucifera is a large, tall and erect palm attaining a height up to 24 metre. Stem is marked with annular leaf scars. Leaves are large, pinnatisect, arranged in the form of a crown. Flowers monoecious in large branched spadix. Perianth segments leathery, valvate. Stamens 6. Pistillode small or absent. Carpels 3, ovary ultimately becomes 1-celled due to abortion of 2 carpels. Fruit a large fibrous drupe. Endosperm oily and watery.

Climate—For better growth coconut plant requires a humid and warm climate having a well-distributed annual rainfall of 100 cm and above. Bright sunshine favours the growth, while cold frost and drought are injurious to the plant.

Soil—Coconut grows best on sandy loams, deltaic alluviums and sandy soils of river valleys. It can also be grown on estuarine deposits, peaty soils and well-drained light black-cotton soils.

Cultivation—Full sized and well-filled nuts of good shape obtained from healthy plants are usually planted at the break of the monsoon in a nursery bed at 30.4 cm distance in rows, rows are 38.0 cm apart. Seedlings grown in this way become ready for permanent planting in the orchard at the age of 9-10 months.

In the meantime the land for orchard should be cleared, levelled and ploughed 3-4 times to get a good tilth. White ant nests, if present in the soil, should be removed by digging. Provision of irrigation channels should also be maintained. Next, 2-3 months before planting, pits measuring 0.9 m × 0.9 m × 0.9 m at distances of 7.6-9.1 metre in straight rows should be dug. Then one year old seedling with the nut still attached are planted in the pits just at the commencement of rains. Just 5-7 days before planting, the pits should be filled up to 30.4 cm depth with a mixture of surface soil ashes and sand. Seedlings are planted in such a way that their nut portions and little part of the collar remain completely within the pits *i.e.* under the soil. After planting, the soil is pressed well around the nut portion and pit is watered. Suitable shades may be provided in case of strong sun rays.

Regular watering and shading in summer are necessary during the first two years. Manuring with 0.21 kg. ammonium sulphate, 0.21 kg. superphosphate and 0.21 kg. muriate of potash before and after the rainy season in each year is essential for young plants. Along with the coconut, vegetables and other fruit trees may be grown.

Coconut tree begins to bear fruits in 6-7 years after planting, full yield commences from the tenth year and continues to produce fruits

up to the age of 50-60 years. For continuous better yield, weeding, ploughing or digging (once or twice a year) and manuring with 1.2-1.6 kg. of ammonium sulphate, 0.8-1.2 kg. of superphosphate and 0.8-1.2 kg. of muriate of potash are essential.

Harvesting and Yield—Harvesting is done in the month of March-May at intervals of 45 or 60 days. Generally, nuts for 'ball' copra are harvested at the dead ripe stage *i.e.* when the fruits start dropping from the tree. For culinary use and 'cup' copra nuts are harvested at the age of 11 months. The average yield in each year per acre varies from 2,000-3,000 nuts, sometimes the yield increases up to 7,000 nuts per acre.

Preparation of Copra and Extraction of Oil—After the fully ripe nuts have been harvested, they are stored unhusked for about one year to make them completely dry. They are then husked, split open and further dried by either natural or artificial heat—as a result dried kernel or copra comes out easily.

Dried kernel is ground up and the oil is extracted from it by cold expression. The oil content of the kernel varies from 50-75%. Coconut oil is pale-yellow in colour or colourless.

Uses—Refined coconut oil is edible—used as cooking oil; also used for making margarine and vegetable ghee. Besides, coconut oil is used as hair-oil and in the preparation of best quality soaps, cosmetics, shampoos etc. and also as an illuminant. The copra residue or oil-cake is used as fodder and as manure.

Varieties—Generally two varieties viz (a) *tall* and the (b) *dwarf* are recognised commonly. The former variety attains a height of 15.5 m or more, takes 5-10 years for fruiting and produces nuts for copra and oil of good quality. The latter variety attains a height of only 7.5-9.0 m, grows slowly and starts fruiting 3 or 4 years after planting; it produces fruits good for culinary use.

Diseases and Insect Pests—

Common diseases are :—(1) True Bud-rot caused by *Phytophthora palmivora*—it can be controlled by destroying the plant to prevent the spread of the disease. (2) Shoot-rot caused by *Gloeosporium* spp.—it can be controlled by spraying the crown with 1% Bordeaux mixture. (3) Leaf-rot caused by *Helminthosporium halodes*, *Colletotrichum paucisetum* and *Gliocladium roseum*—control measure is not yet known.

Common insect pests are :—(1) Coconut black beetle or Rhinoceros beetle (*Oryctes rhinoceros*)—it can be controlled by burning of all decaying refuse. (2) Coconut caterpillar (*Nephantis serinopa*)—can be controlled by cutting and burning infested leaves.

12.6 A Few Important Oil and Oil-yielding Plants

(a) **NIGER OIL** (*Sarguza*, *Ramtil*) : It is obtained from the seeds of *Guizotia abyssinica* (L. f.) Cass, of the family Compositae.

The plant is a herb, native of tropical Africa. It is cultivated extensively in India, Germany, tropical Africa and the West Indies. In India, niger plant grows in Madhya Pradesh, Andhra Pradesh,

Mysore and Orissa—the annual area under cultivation is 8 lakh acres and the annual production 93,000 tonnes.

The oil content of seed varies from 38—50%, the oil is semi-drying type, pale-yellow and has a pleasant aromatic odour. Niger oil of higher grade is used for soap making, lighting, lubrication and as drying oil. The seed-cake is used as fodder.

The crop is sown in July-August and harvested during November—January ; it grows best on light loam soils.

(b) **SAFFLOWER OIL (*Kusum, Barre*)** : It is obtained from the seeds of *Carthamus tinctorius* L. of the family Compositae.

The plant is an annual herb, native of Abyssinia and Afghanistan. In India it is cultivated mainly in Maharashtra, Andhra Pradesh, Mysore and Madhya Pradesh—the annual area under cultivation is 10·9 lakh acres and the annual production 20 lakh tonnes.

The oil content of the seed varies from 24-36%. The cold pressed oil is golden-yellow in colour and edible. Safflower oil is a drying oil and has a high linoleic acid content (about 75%) but contains very little linolenic acid.

This oil is also used for making soaps, paints, varnishes and linoleum.

Safflower is sown in October-November and is harvested during February-April.

It grows well on water-retentive black soils and alluvial loams.

(c) **SESAME OIL (*Til, Gingelly*)** is obtained from the seeds of the plant *Sesamum indicum* L. of the family Pedaliaceae.

The plant is an annual herb, native of India. In India, the crop is cultivated mainly in U. P., Madhya Pradesh, Rajasthan, Andhra Pradesh, Tamil Nadu and Maharashtra. Other important sesamum producing countries are China, Manchuria, Pakistan, Burma, Sudan, Mexico and Turkey. In India, sesamum is one of the important oil-seed crops—the annual area under cultivation is about 6·1 million acres and the annual production 5,00,000 tonnes.

The oil content of the seed varies from 46—52%. Sesame oil is of the semi-drying type. It contains about 40 per cent each of oleic and linoleic acid and about 14 per cent saturated fatty acids. Sesame oil is used as a cooking oil in South India, It is also used for anointing the body, in the manufacture of perfumery oils, soap and cosmetics. Oilcake is used as fodder.

Sesame is sown either in June-July or in April-May and harvested within 3-6 months after sowing. The plant grows best on well-drained light loam soils.

Sugar-yielding Plants

Sugars are soluble carbohydrate food-matters *e.g.* glucose ($C_6H_{12}O_6$), fructose ($C_6H_{12}O_6$), sucrose ($C_{12}H_{22}O_{11}$) etc. All autophytic plants manufacture sugars; most of such sugars are directly used by plants in their metabolism—hence little portion is stored in various plant organs. In some plants *e.g.* beets, sugarcane, sugar maple, fan palms, in flowers and fruits of many plants etc. storage sugars are to be found—these reserved sugars obviously serve as the chief sources of sugars for human food. Sugar, obtained from different types of plants, form one of the most essential and valuable plant products of the world. The name “sugar” has been derived from the Sanskrit word “*sarkara*” which means gravel, and refer to the crude sugar.

13.1 Sugarcane (*Akh, Seesal*): At present the main source of sugar is the sugarcane plant *Saccharum officinarum* L. belonging to the family Gramineae.

Sugarcane plant probably originated in South-Eastern Asia or the East Indies from some wild ancestor of that region. In India, the plant is very ancient one and was known by 327 B. C.

In India, sugarcane is grown mainly in U. P., Bihar and the Punjab. It is also cultivated in Maharashtra, Andhra Pradesh, Tamil Nadu, Madhya Pradesh and W. Bengal. The annual area under the cultivation of this crop is about 6 million acres and the production of raw sugar is about 8 million tonnes. Besides India, other sugar producing countries are Bangladesh, Pakistan, Brazil, Cuba, Mexico, Central and South America, West Indies, Australia etc.

Saccharum officinarum is a tall and vigorous perennial grass reaching a height of 2.5-3.6 metres under proper cultivation. Stem bamboo-like, solid with a tough rind and numerous fibrous strands and sweet sugary juice. Leaves long flat with thick midrib. Spikelets paired—the primary is pediceled, the secondary is sessile, awnless with short callus covered with long hairs in large spreading spicate panicle; rachis long and hairy usually. Lower basal glume small, papery membranous, lower lemma very narrow or absent; palea ciliate, nerveless, upper floret bisexual. Lodicules smooth.

Climate—Sugarcane grows well in tropical humid regions having a well-distributed rainfall of 623-1,200 mm per annum and a temperature ranging between 25°C-50°C.

Soil—Sugarcane can be grown on all types of soil, but it grows well on medium heavy loams and clay loams of the Gangetic and other alluvium. Brown or reddish loams, laterites and black cotton soils are also suitable for sugarcane cultivation.

Rotation—Sugarcane is grown in rotation with paddy, wheat, cotton, gram, maize, peas and other garden crops like potatoes, chillies, onion, turmeric etc.

Cultivation—The land is neatly and thoroughly prepared by one or two deep ploughings—these should be followed by clod-crushing by a clod-crusher or a disc-harrow. Compost, cattle-manure and other organic manures should be applied well in advance to the land before planting. Sugarcane is propagated by 30-50 cm long 3-budded stalks or cuttings (made from the upper joints of old canes)—these are known as '*setts*' or *seeds*. These stalks are generally selected from healthy and free from diseases and pests. Planting is generally done with the advent of warm weather after the cold season during the months of February to March.

There are three methods of planting *viz.*, (1) flat planting, (2) furrow planting and (3) trench planting.

1. *Flat planting*—In this case shallow furrows are made by plough 80—100 cm apart ; seeds or *setts* are placed in shallows end to end and covered with 5—7 cm of soil—then the field is levelled up with a beam. The field is then irrigated by spreading water.

2. *Furrow planting*—In this method, furrows in the field are made by means of a ridger about 10-15 cm or 20 cm deep. Then *setts* are placed end to end or otherwise in furrows and covered with the soil at a depth of 5.7 cm in such a way that the upper portion of the furrow is left unfilled. Immediately after these operations, water is let into furrow.

3. *Trench planting*—In this type, rectangular and 20-25 cm deep trenches are made—the bottom of the furrow is then dug up and loosened, next shallow pits or furrows are made in the bed of the trench where *setts* are laid end to end or otherwise ; *setts* are then covered with 5-7 cm of soil. Then water is let into the trenches.

There are two systems of planting e.g. dry and wet. In dry system sugarcane is not irrigated at the time or immediately after planting while in wet system the field is irrigated either before or immediately after planting so that *setts* germinate in wet soil.

For high yield, proper irrigation is essential specially in areas where there is no well-distributed rainfall. Regular hoeing and weeding should be given to the crop—the first operations are generally given 3-4 weeks after planting. Sugarcane should be manured adequately with nitrogen (130-500 kg. per hectare) and P_2O_5 (40-50 kg. per hectare). Green manuring at the rate of 100-150 quintals per hectare also increases the yield.

Ripening and Harvesting—Sugarcane begins to ripen from December to March. At maturity, the lower leaves gradually dry up by leaving few green leaves at the top. At the time of harvesting, stalks are cut at the ground level—then dry leaves are stripped off and stalks are topped at the topmost mature internode. Harvested stalks

are tied up in bundles and despatched to the market in fresh condition for direct consumption or to the sugar mills for the manufacture of 'gur' and sugar. The sugar content of canes varies from 75-80%.

Yield—The yield of one year crop under normal conditions of cultivation varies in different States e.g. 35 tonnes of cane per hectare in U.P., Bihar, Punjab, Rajasthan and Assam; 60-80 tonnes per hectare in Maharashtra, Tamil Nadu, Mysore and Andhra Pradesh; 30-50 tonnes per hectare in W. Bengal, Orissa and Kerala. These yields may become double under good conditions of manuring and irrigation.

Extraction and Manufacture of Sugar—Sugarcane stalks, after harvesting, are carried to mills where they are crushed into small pieces. Then small pieces are passed through three sets of rollers where all the sap is gradually extracted leaving the bone-dry residue called '*bagasse*'. The crude extract is a dark-greyish sweet liquid full of impurities which contains sucrose and other sugars together with gums, proteins, colouring matters, acids, dirt and sometimes pieces of cane. Then through *defecation* and *clarification* processes, the crude extract is purified—in the former process, separation of the insoluble materials is done while in 'clarification' process, precipitation of soluble non-sugars is made. The juice is filtered to remove the solid particles—it is then heated to coagulate the proteins. Then lime is added to neutralise the acids, to precipitate CaCO_3 and to prevent the conversion of sucrose to other undesirable sugars—sometimes CO_2 is added to assist in the process. After these operations, the juice becomes clear and dark-coloured which is then boiled in open kettles or vacuum pans to a sticky syrup known as *massecuite*. Next *massecuite* is placed in hogsheads with perforated bottoms where the juice slowly percolates through the perforations leaving behind the crystallised sugar. The percolated juice forms the mollasses of commerce.

Uses—Cane sugar is used variously e.g. in the preparation of sweets, syrup, jam, jelleys etc., in making all sorts of beverages, ir cooking etc. The by-products of sugar industry are commercially used for molasses, rum, industrial alcohol and synthetic rubber; molas-cuit (a mixture of bagasse or refuse canes and molasses) is used as fodder. Bagasse is used also in the manufacture of bagpaper, wrapping, writing and printing papers, cardboard etc.

Varieties—The improved varieties recommended for cultivation in different States of India are as follows :—

1. W. Bengal—Co. 313, and B.O. 11 (early varieties); Co. 419, Co. 617, B.O. 14, B.O. 17, B.O. 29, B.O. 32 (Mid and late varieties)
2. Bihar—Co. 313, B.O. 3, B.O. 10, B.O. 34, B.O. 43 (early var.); Co. 419, Co. 617, B.O. 14, B.O. 17, B.O. 29, B.O. 32 (mid and late var.)
3. Uttar Pradesh—Co. 313, Co. 395, Co. 859, B.O. 10, Co. S. 416, Co. S. 510, Co. S. 541 (early var.); Co. 356, Co. 393, Co. 421, Co. 527, Co. 846, Co. 1007, Co. 1158, B.O. 3, B.O. 17, B.O. 32, Co.S. 109, Co.S. 245, Co.S. 443, Co.S. 568, Co.S. 575 (Mid and late var.)

4. Madhya Pradesh—Co.S. 245 and Co.S. 321 (early var.) ; Co. 419, Co. 421 Co. 617, Co. 678, Co. 683, Co. 775, Co. 779, Co. 110; (mid and late var.)
5. Maharashtra—Co. 740, Co. 775 (early var.) ; Co. 419, Co. 678, Co. 798 (mid and late var.)
6. Andhra Pradesh—Co. 527, Co. 997 (early var.) ; Co. 419, Co. 449, Co. 467, Co. 975 (mid and late var.)
7. Tamil Nadu—Co. 527 (early var.) ; Co. 419, Co. 449 (mid and late var.)
8. Orissa—Co. 881 (early var.) ; Co. 419, Co. 421, Co. 872, Co. 897 (mid and late var.)
9. Assam—Co. 313 (early var.) ; Co. 419, Co. 421, Co. 449 and P.O.J. 2714 (mid and late var.)
10. Punjab—Co. 313, Co.L. 29 (early var.) ; Co. 312, Co. 421, Co. 453, Co.L. 9, Co.J. 39 and Co.J. 46 (mid and late var.)

Diseases and Insect Pests—

Common diseases are : (1) Red rot caused by *Glomerella tucumanensis*—it can be controlled by growing resistant varieties, removing affected canes etc. (2) Red strip caused by *Pseudomonas rubrilineans*—can be controlled by the application of ammonium nitrate before monsoon, also by removing affected clumps. (3) Bunga caused by *Aeginetia indica*—can be controlled by removing infected shoots with parasite and burn. (4) Eye spot caused by *Helminthosporium sacchari*—can be controlled by growing resistant varieties. (5) Mosaic and Grassy shoot virus diseases—former can be controlled by growing resistant varieties and by selecting healthy setts, the latter can be controlled by treating seeds with hot water (52°C for one hour) and also by selecting healthy seeds.

Common insect pests are :—(1) Top shoot borer (*Scirpophaga nivella*)—can be controlled by removing and destroying top shoots infested with pest. (2) Stem borers (*Chilotraea* spp.)—can be controlled by using setts free from borer and light traps, water-shoots also to be removed. (3) Root borer (*Emmalocera depressella*)—can be controlled by digging out and destroying stubbles after harvest. (4) Leaf hopper (*Pyrilla perpusilla*)—can be controlled by destroying nymphs and adults, and by spraying with 0.25% BHC at 425–637 litres per acre.

13.2 Sugar-beet (Beet) : Another important sugar-yielding plant is sugar-beet. About 45 per cent of the total world production of sugar is estimated to come from sugar beet. Sugar is obtained from the roots of sugar-beet plant. Sugar-beet was known long before the beginning of Christian era as a source of sugar. The sugar from sugar-beet was first manufactured in France and Germany in 1800. At present, the sugar industry in most of the western countries viz. Belgium, Denmark, France, Germany, the Netherlands, Sweden, the U.S.A. and the U.S.S.R. is solely dependant of sugar-beet.

In India sugar-beet was cultivated during British regime in the North West Frontier Province. At present an intensive and extensive effort is being made to extend and popularise sugar-beet cultivation in India.

Botanically sugar-beet is known as *Beta vulgaris* L. var. *rapa* Dum. belonging to the family Chenopodiaceae. Plant is a white rooted biennial herb.

Climate—For better growth, sugar-beet requires cool climate having a temperature range of 18°C–22°C with good rainfall or irrigation (50–60 cm) and bright sunshine.

Soil—Sugar-beet grows in all good types of soils—generally sandy loam or loam are preferred for better growth. It does best in neutral or slightly alkaline soils.

Cultivation—Because of its climatic requirements sugar-beet can be grown in India only during the *rabi* season—specially in the Northern and Western plains. A good, firm, well levelled seed bed, free from clods and stubbles, with sufficient moisture is necessary for proper cultivation of sugar-beet. The optimum time of sowing for better yield is from end September to early October, delay greatly reduces yield. Sugar-beet can be sown either on flat beds or on ridges. A seed rate of about 10 kg. per hectare has been found to give satisfactory stand of the crop. The seeds are sown either by dibbling or dropping in shallow furrow 2-4 cm deep at intervals of 3-5 cm, to be thinned subsequently at the 4-leaf stage to about 20-25 cm between plants. The rows are spaced 40-45 cm apart. After sowing the seeds are covered quickly with soil and if sufficient moisture is not prevailing in soil, an irrigation should be given in the furrows, taking care that the water does not reach the top of the ridges. The sugar-beet crop requires a total of 8-10 irrigations depending on soil type and weather conditions; generally one irrigation is given every 15-20 days. The sugar-beet field should be kept free from weeds by weeding as often as necessary. Normally the crop is weeded 2-3 times. Sugar-beet is a heavy feeder of plant nutrients; a soil of average fertility requires about 100 kg. nitrogen and 90 kg. phosphoric acid per hectare. Fifty per cent of the total nitrogen may be applied as farmyard manure and the other half in the form of urea, ammonium sulphate or calcium ammonium nitrate. The farmyard manure and phosphate is applied 2-3 weeks before sowing and the inorganic nitrogen fertilizer is given as top dressing in two doses, one after thinning and the other before end of January.

Harvesting and Yield—The crop is ready for harvest by about the middle of April—when many of the lower leaves dry up. However, the crop can be harvested from the middle of March to end of May. The plants are lifted by hand and the roots are shaken free of soil. The shoots are cut a little above the position of the largest circumference of the roots.

In the temperate countries the average yield of fresh beet roots ranges between 30 and 50 metric tonnes per hectare. In India, though sugar-beet cultivation is not done on commercial basis at present, but in cropping tests yields ranging between 35 and 40 metric tonnes on an average, have been obtained.

Varieties : Only imported varieties have so far been grown in India. Of these Ero type E (West German), US 35 and US 75 (American), Ramonskaya (Russian), Triplex, Bush E (English), Maribo Anglo Poly, Maribo Resista Poly and Maribo Magna Poly (Danish) have been found to do well under Indian conditions.

Extraction of Juice—Harvested roots are cleaned and cut into pieces and then heated in running water in a series of tanks—in this

process known as diffusion process, about 97% of sugar is extracted. Next, insoluble impurities in the raw juice are removed by carbonation process (in which the raw juice is treated with lime so that CaCO_3 precipitates and other non-sugars become coagulated). Then purified juice is separated out by filtration. After filtration, clear juice is obtained which is concentrated, crystallised and centrifuged.

Uses—Beet sugar is consumed in the same way as cane sugar. Its by-products are used variously such as pulp (dried or wet) used as cattle feed, the filter cake used as manure and the molasses used for cattle feed and in the manufacture of alcohol.

Diseases and Insect Pests—

Beet is attacked by a number of diseases and insect pests. Among the fungal diseases rhizoctonia root rot, sclerotium root rot and cercospora leaf spot are important. Curly top and yellowing are caused by virus. The spread of virus diseases may be restricted by controlling the insect vectors (aphids) through application of 0.1% Malathion E.C. But it is advisable to rogue out and destroy the affected plants, if detected early when the disease is confined to a few plants.

Cutworms and hairy caterpillars are the most damaging insect pests. The former can be controlled by soil application of Heptachlor @ 0.6 kg. per hectare, while the latter may be controlled by using 10% BHC dust @ 12-15 kg. per hectare (or 5% BHC dust @ 20 kg. per hectare).

13.3 Palmyra Palm or Fan Palm (*Tal, Tar*): The botanical name of Palmyra or Fan Palm is *Borassus flabellifer* L. belonging to the family Palmae.

B. flabellifer is a native of tropical Africa. In India, this plant is found to grow along the coastal areas of the Peninsula, W. Bengal, Bihar and Orissa.

B. flabellifer is a tall unbranched tree attaining a height of 12-18 m and a girth of 1.0-2.0 m. Leaves are large, fan-like, forming a crown at the apex of the stem. The stem is black, outer hard portion is composed of stiff longitudinal fibres. Inflorescence large, mixed spadix type. Flowers unisexual, monoecious. The fruit is large and fibrous, containing 3-nut-like portions, each of which encloses a seed.

The palmyra palm is one of the important toddy yielding palms. Palmyra toddy contains a little amount sugar (2.5 gms. of sugar in 100 cc. of sap) and vitamin B. But *nira* tapped from the tree is sweet, transparent and pleasant smelling. Toddy is a pale forthy liquid having a pungent and a slightly acidic taste—it is used largely as refreshing beverage by the lower classes. The sucrose contained in *nira* is also used in making '*Tal gur*'.

Diseases and Insect Pests—Palmyra palm is attacked by a fungus disease called 'bud-rot', caused by *Pythium palmivorum*.

Among the insect pests, attacks of rhinoceros beetle (*Oryctes rhinoceros*), the red-palm weevil (*Rhynchophorus ferrugineus*), the black headed caterpillar (*Nephantis serinopa*) are common.

List of Economically Important Plants and Their Uses :—

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
1. Plants yielding Cereals and Millets				
Barley (Job, Jau)	<i>Hordeum vulgare</i> L.	Gramineae	Endosperm, of the grain i.e. Caryopsis (fruit)	As food (Cereal)
Barnyard or Shama millet (Shyama, Sanwa)	<i>Echinochloa colonum</i> (L.) Link.	"	"	" (Millet)
Broomcorn	<i>Sorghum vulgare Pers. var. technicum</i>	"	"	" (Millet)
Buck-wheat (Kutu)	<i>Polygonum fagopyrum</i> L.	Polygonaceae	Seeds or groats of achene	As food (Pseudo-cereal) As food (Millet)
Bulrush millet or Pearl millet (Bajra)	<i>Pennisetum typhoides</i> (Burm. f) Stapf & Hubb.	Gramineae	Endosperm of the grain i.e. Caryopsis (fruit)	"
Finger millet (Marwa, Ragi, Mandal)	<i>Eleusine coracana</i> (L.) Gaertn.	"	"	"
Fox-tail or Italian millet (Kaon, Kakum)	<i>Setaria italica</i> (L.) Beauv.	"	"	"
Great millet (Jowar, Jaur)	<i>Andropogon sorghum</i> Brot.	"	"	"
Indian oat, Red oat (Jai)	<i>Avena sterilis</i> L. var. <i>culta</i>	"	"	" (Cereal)
Japanese millet (Sanwa, Sawa)	<i>Echinochloa frumentacea</i> (Roxb.) Link.	"	"	" (Millet)
Job's tear millet (Gargari)	<i>Coix lacrymna-jobi</i> L.	"	"	"
Kodo millet (Kodo, Kodon)	<i>Paspalum scrobiculatum</i> L.	"	"	"
Little millet (Kutki)	<i>Panicum miliare</i> Lamk.	"	"	"
Maize (Bhutta, Makka)	<i>Zea mays</i> L.	"	"	" (Cereal)
Oats (Jai, Jale)	<i>Avena sativa</i> L.	"	"	"
Proso, Hog or Common millet (Cheena, Barri)	<i>Panicum miliaceum</i> L.	"	"	" (Millet)
Rice or Paddy (Dhan, Chawal)	<i>Oryza sativa</i> L.	"	"	" (Cereal)

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Rye	<i>Secale cereale</i> L.	Gramineae	Endosperm of the grain i.e. Caryopsis (fruit)	As food (Cereal)
Sorghum (Jowar)	<i>Sorghum vulgare</i> Pers.	"	"	" (Millet)
Wheat (Gm, Gehlon)	<i>Triticum aestivum</i> L.	"	"	" (Cereal)
II. Plants yielding Pulses				
Black gram (Maskakai, Urd)	<i>Phaseolus mungo</i> Roxb.	Leguminosae (Papilionaceae)	Cotyledons or seeds as a whole of the legume fruit	As pulse food
Chikling vetch (Grass pea, Khesari)	<i>Lathyrus sativus</i> L.	"	"	"
Dew gram or Moth bean (Meth-kalai)	<i>Phaseolus aconitifolius</i> Jacq.	"	"	"
Field pea (Desi matar, Mutter)	<i>Pisum sativum</i> L. var. <i>arvense</i> Poir.	"	"	"
Garden pea (Gol matar, Mutter)	<i>Pisum sativum</i> L.	"	"	"
Gram or Chick pea (Chola, Chana)	<i>Cicer arietinum</i> L.	"	"	"
Green gram or Mung bean (Sona mung, Moong)	<i>Phaseolus aureus</i> Roxb.	"	"	"
Horse gram (Kulthikalai)	<i>Dolichos biflorus</i> L.	"	"	"
Lentil (Masur, Musuri)	<i>Lens culinaris</i> Medic.	"	"	"
Pigeon pea (Arhar)	<i>Cajanus cajan</i> (L.) Millsp.	"	"	"
Rice bean	<i>Phaseolus calcaratus</i> Roxb.	"	"	"
III. Plants yielding Vegetables				
A. Legume Vegetables :—				
Adzuki bean	<i>Phaseolus angularis</i> Roxb.	"	Young fruits (legumes or pods) and seeds	As a vegetable food
Broad bean (Baklashim, Baakla)	<i>Vicia faba</i> L.	"	Seeds of the pods	Eaten as vegetable

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Cluster bean or Field vetch (Guar)	<i>Cyamopsis tetragonoloba</i> (L.) Taub.	Leguminosae (Papilionaceae)	Young fruits (pods) and seeds	Eaten as vegetable
Cowpea (Barbati, Choli-lobia)	<i>Vigna sinensis</i> (L.) Savi ex Hassk.	"	"	"
Faraz bean or French bean or Kidney bean (Rajmanh.	<i>Phaseolus vulgaris</i> L.	"	Young fruits (pods)	"
Florida velvet bean (Tarukala or Toharshim)	<i>Mucuna deeringiana</i> (Bort.) Merr.	"	The young fruits (pods)	"
Goa bean (Charakonishim, Chaudhaari-phali)	<i>Psychocarpus tetragonolobus</i> (L.) DC	"	"	"
Hyacinth bean or Lablab bean or Indian bean (Deshishim, Shim)	<i>Dolichos lablab</i> L.	"	The green pods and seeds	"
Jack or Sword bean (Makhan- shim)	<i>Canavalia gladiata</i> (Jacq.) DC.	"	Pods i.e. fruits	"
Lima bean (Ban barbati, Lo- biya) or Sieva bean or Double bean	<i>Phaseolus lunatus</i> L.	"	The young pods and seeds	As vegetable and pulse
Lion bean (Kumach or Toharshim)	<i>Mucuna cochinchinensis</i> (Lour.) Chev.	"	Pods (fruits)	As vegetable
Molucca bean (Karanju)	<i>Caesalpinia crista</i> L.	Leguminosae (Caesalpiniae)	"	"
Nicker bean (Gilla, Barabi)	<i>Entada phaseoloides</i> (L.) Merr.	Leguminosae (Mimosae)	Seeds of the fruits (woody lomentum)	Edible
Soybean (Garikalai, Bhat)	<i>Glycine hispida</i> , G. max (L.) Merr.	Leguminosae (Papilionaceae)	Seeds of pods	Used as vegetable and pulse
Scarlet runner bean	<i>Phaseolus coccineus</i> L.	"	"	Used as vegetable
Yam bean (Sakalu)	<i>Pachyrhizus erosus</i> (L.) Urb.	"	"	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
B. Earth Vegetables :—				
ROOTS :				
Beets or Beet root (Beet, Chukandar, Mangles etc.)	<i>Beta vulgaris</i> L.	Chenopodiaceae	The roots (Napiform)	Cooked roots are used as vegetable
Carrot (Gajar)	<i>Daucus carota</i> L.	Umbelliferae	„ (Conical)	„
Cassava or Tapioca (Sakar-kanda)	<i>Manihot esculenta</i> Crantz	Euphorbiaceae	„ (Tuberous)	„
Chard	<i>Beta vulgaris</i> L. var. <i>cicla</i>	Chenopodiaceae	„ (Napiform)	„
Oyster plant or Salsify	<i>Tragopogon portifolium</i> L.	Compositae	The roots	„
Parsnip (Gujar)	<i>Pastinaca sativa</i> L.	Umbelliferae	„	„
Radish (Mula, Mooli)	<i>Raphanus sativus</i> L.	Cruciferae	„ (Fusiform)	„
Rutabagas or Swedes	<i>Brassica napobrassica</i> L.	„	„	„
Sugar beet (Mitha beet)	<i>Beta vulgaris</i> L. var. <i>rapa</i> Dum.	Chenopodiaceae	„ (Napiform)	„
Sweet potato (Mishri alu, Shakarkandi)	<i>Ipomoea batatas</i> Poir.	Convolvulaceae	„ (Tuberous)	„
Turnip (Shalgam)	<i>Brassica rapa</i> L.	Cruciferae	„ (Napiform)	„
Yams (Chupri alu, Rota aloo)	<i>Dioscorea alata</i> L.	Dioscoreaceae	„ (Tuberous)	„
STEMS :				
Annu	<i>Tropaeolum tuberosum</i> L.	Tropaeolaceae	Tuberous stem	Used as vegetable
Elephant ear (Edible arum, Kachu)	<i>Colocasia esculenta</i> (L.) Schott.	Araceae	Stem (Tuberous rhizome)	„
Garlic (Rasun, Lashun)	<i>Allium sativum</i> L.	Liliaceae	Stem (bulbs)	Used as vegetables and condiment

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Jerusalem artichoke (Hathi-chuk)	<i>Helianthus tuberosus</i> L.	Compositae	Tuberous stem	Used as vegetable
Leek (Gandina)	<i>Allium porrum</i> L.	Liliaceae	Bulbs	"
Oca	<i>Oxalis tuberosa</i> L.	Oxalidaceae	Tuberous stem	"
Onion (Piaj, Piaz)	<i>Allium cepa</i> L.	Liliaceae	Fleshy leaf bases together with bulb	"
Potato (Alu, Aaloo)	<i>Solanum tuberosum</i> L.	Solanaceae	Tuberous stem	"
Telugu potato or Elephant-foot yam (Ol, Zamin-kand)	<i>Amorphophallus campanulatus</i> Bl.	Araceae	Stem (Corm)	"
Ullucu or Melloco	<i>Ullucus tuberosus</i> Caldas	Basellaceae	Tuberous stem	"
Yautias	<i>Xanthosoma sagittifolium</i> Schott.	Araceae	Rhizomatous stem	"
C. Herbage Vegetables :—				
Amaranth (Ban natey)	<i>Amaranthus oleraceus</i> L.	Amaranthaceae	Leaves	"
"	<i>A. blitum</i> L.	"	"	"
" (Natey sag)	<i>A. caudatus</i> L.	"	"	"
" (Shada natey)	<i>A. blitum</i> L. var. <i>oleraceus</i> Hk.f.	"	"	"
Bladderdock (Chuck or Tak palang)	<i>Rumex vesicarius</i> L.	Polygonaceae	"	"
Borecole or Kale (Karam-sag)	<i>Brassica oleracea</i> L. var. <i>acephala</i> DC.	Cruciferae	Young shoots and leaves	"
Brussels sprouts (Buttom gobi)	<i>B. oleracea</i> L. var. <i>gemmifera</i> Zenk.	"	Young shoots, buds and leaves	"
Cabbage (Bandha kapi, Patgobhy)	<i>B. oleracea</i> L. var. <i>capitata</i> L.	"	Enlarged terminal bud	"
Cauliflower (Phool gobi, Phulkapi)	<i>B. oleracea</i> L. var. <i>botrytis</i> L.	"	Entire immature inflorescence of abortive flower (head)	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS		MAIN USES
			Leaf-stalks	As vegetable	
Celery (Ajmund)	<i>Apium graveolens</i> L. var. <i>duice</i> DC.	Umbelliferae	Leaf-stalks	As vegetable	
Chicory (Kasni)	<i>Cichorium intybus</i> L.	Compositae	Leaves	"	
Cress (Halim or Aleveri)	<i>Lepidium sativum</i> L.	Cruciferae	Seeds	"	
Drumstick (Sajina, Segaa)	<i>Moringa oleifera</i> Lamk.	Moringaceae	Green fruits	"	
Eradiv (Kasni)	<i>Cichorium endivia</i> L.	Compositae	Leaves	"	
Garden asparagus	<i>Asparagus officinalis</i> L.	Liliaceae	Shoots	"	
Globe-artichoke (Hathichuk)	<i>Cynara scolymus</i> L.	Compositae	Leaves and young flower-heads	"	
Goosefoot (Bathua)	<i>Chenopodium album</i> L.	Chenopodiaceae	Tender twigs and leaves	"	
Kohlrabi or Kaolkhol (Ganth gohiy, Olkapi)	<i>Brassica oleracea</i> L. var. <i>gongylodes</i> L.	Cruciferae	Enlarged and juicy stem	"	
Lettuce (Letus, Salad)	<i>Lactuca sativa</i> L.	Compositae	Leaves	"	
Mountain spinach or Orach (Chakwai)	<i>Atriplex hortensis</i> L.	Chenopodiaceae	Branches and leaves	"	
Mustard leaf	<i>Brassica campestris</i> L. var. <i>satson</i> Prain ; <i>B. juncea</i> (L.) Cz. & Coss. var. <i>cuneifolia</i> Roxb. ; <i>B. hirta</i> Moench etc.	Cruciferae	Tender twigs and leaves	"	
Purslane (Nunia sag, Kulfa)	<i>Portulaca oleracea</i> L.	Portulacaceae	Leaves	"	
Rhubarb	<i>Rheum rhaponiticum</i> L.	Umbelliferae	Succulent acidic leaf-stalks	"	
Spinach (Palang, Palak)	<i>Spinacia oleracea</i> L.	Chenopodiaceae	Leaves	"	
Tampala (Lal sag)	<i>Amaranthus tricolor</i> L.	Amaranthaceae	Leaves	"	
Water cress (Brahmi sag)	<i>Nasturtium officinale</i> R. Br.	Cruciferae	Leaves	"	
Wild cabbage	<i>Brassica oleracea</i> L.	"	Entire immature inflorescence	"	
D. Fruit Vegetables :—					
Ash or white gourd (Chal-kumra, Petha)	<i>Benincasa hispida</i> Cogn.	Cucurbitaceae	Mesocarp and endocarp of the fruit (Pepo)	"	

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Avocado, or Alligator pear (Khubani, Avocado)	<i>Persea americana</i> Mill.	Lauraceae	Pulp (mesocarp) of the pear-shaped fruit (one-seeded Berry)	As vegetable
Bitter gourd (Karala)	<i>Momordica charantia</i> L.	Cucurbitaceae	Entire fruit when young (Pepo)	"
Balsam apple (Mokha)	<i>Momordica balsamina</i> L.	"	"	"
Bottle gourd (Lau, Lauki)	<i>Lagenaria siceraria</i> Standl.	"	"	"
Breadfruit (Khadel)	<i>Artocarpus communis</i> Forst.	Moraceae	Mesocarp and endocarp of young fruit (Pepo)	"
Chillies or Red pepper (Lanka, Lal-mich)	<i>Capsicum frutescens</i> L.	Solanaceae	Perianth, seed and bracts of the fruit (Sorosis)	"
Choco, chayote (Quash)	<i>Sechium edule</i> Sw.	Cucurbitaceae	Perianth and placenta bearing seeds of the fruit (Berry)	"
Cucumber (Shasha, Kheera)	<i>Cucumis sativus</i> L.	Cucurbitaceae	Entire fruit (berry-like) is edible	"
Egg plant or Brinjal (Begun, Baigon)	<i>Solanum melongena</i> L.	Solanaceae	Entire fruit (Pepo) when young	"
Fig (Dumrur, Anjeer)	<i>Ficus carica</i> L.	Moraceae	Entire fruit (Berry)	"
Jack fruit (Kathal)	<i>Artocarpus heterophyllus</i> Lamk.	"	Fleshy receptacle of the fruit (Syconus)	"
Kankrol or Bhat Karala	<i>Momordica cochinchinensis</i> Spreng.	Cucurbitaceae	Pericarp, perianth and seed of the green fruit (Sorosis)	"
Little gourd (Telakuch, Kundrou)	<i>Coccinia indica</i> W. & A.	"	Entire fruit (Pepo)	"
Okra or Lady's finger (Bhindi, Dherash)	<i>Abelmoschus esculentus</i> Moen.	Malvaceae	" (Capsule)	"
Pointed gourd (Patol, Parwal, Palwal)	<i>Trichosanthes dioica</i> Roxb.	Cucurbitaceae	Mesocarp and endocarp of the fruit (Pepo)	"
Pumpkin or Summer squash (Kumra, Safed kadu)	<i>Cucurbita pepo</i> L.	"	" (Pepo)	"
Red pumpkin or Winter squash (Sita phal, Kumra)	<i>Cucurbita maxima</i> Duch.	"	"	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Ridge gourd (Jhinga, Tori)	<i>Luffa acutangula</i> (L.) Roxb.	Cucurbitaceae	Mesocarp and endocarp of the fruit (Pepo)	As vegetable
Small bitter-gourd (Ucchey, Murela)	<i>Momordica dioica</i> Roxb. ex. Wild	"	Entire fruit (Pepo)	"
Smooth gourd (Dhundul, Kali tori)	<i>Luffa cylindrica</i> (L.) Roem.	"	Mesocarp and endocarp of the fruit (Pepo)	"
Snake gourd (Chichinga)	<i>Trichosanthes anguina</i> L.	"	" "	"
Squash (Mishiti kumra, Mitha kadu)	<i>Cucurbita moschata</i> Duch. ex. Poir.	"	" "	"
Tomato (Bilati begun, Tamatter)	<i>Lycopersicon esculentum</i> Mill.	Solanaceae	Entire fruit i.e. pericarp and placenta bearing seeds (Berry)	"
IV. Plants yielding Fruits				
Almond (Badam)	<i>Prunus amygdalus</i> Betsch	Rosaceae	Epicarp and mesocarp of the fruit (Drupe)	Eaten as raw fruits
Apple (Apel, Set)	<i>Malus sylvestris</i> (L.) Mill.	"	Fleshy thalamus of the fruit (Pome)	"
Apricot (Khubani)	<i>Prunus armeniaca</i> L.	"	Pericarp of the fruit (Drupe) and also cotyledons of seed	"
Black berry (Bilati anchu)	<i>Rubus fruticosus</i> L.	"	Epicarp and mesocarp of the fruit (Drupe)	"
Black plum or Java Plum or Jambolana (Jam, Jamun)	<i>Syzygium cumini</i> (L.) Skeels	Myrtaceae	Pericarp together with thalamus (Berry)	"
Banana (Kela, Paka kala)	<i>Musa paradisiaca</i> L.	Musaceae	Mesocarp and endocarp of the fruit (Berry)	"
Bullock's-heart or Common custard apple (Nona or Ramphal)	<i>Annona reticulata</i> L.	Annonaceae	Pericarp of the aggregate fruit (Etaerio of berries)	"
Cape-gooseberry (Tepari, Rasbari)	<i>Physalis peruviana</i> L.	Solanaceae	Pericarp of the fruit (Berry)	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY	
			IMPORTANT PARTS	MAIN USES
Carambola (Kamranga, Kam-rakn)	<i>Averrhoa carambola</i> L.	Oxalidaceae	Entire fruit, except seeds (Berry)	As raw fruits
Cashew (Kaju Badam, Kaju)	<i>Anacardium occidentale</i> L.	Anacardiaceae	Cotyledons of the seed (Nut)	"
Cherry (Gilas)	<i>Prunus avium</i> L.	Rosaceae	Epicarp and mesocarp of the fruit (Drupe)	"
Citron (Baro lebu or Nimbu)	<i>Citrus medica</i> L.	Rutaceae	Juicy hairs developing from the inner wall of endocarp of the fruit (Hesperidium)	"
Coconut (Narikel, Narya)	<i>Cocos nucifera</i> L.	Palmae	Endosperm and cotyledon of the fruit (Fibrous drupe)	"
Custard apple or Sweet sop or Sugar apple (Ara, Sitaphal, Sharifa)	<i>Annona squamosa</i> L.	Annonaceae	Pericarp of the aggregate fruit (Etaerio of berries)	"
Date palm (Khejur, Pind-khajur)	<i>Phoenix dactylifera</i> L.	Palmae	Mesocarp of the fruit (Drupe)	"
Delicious monster or Ceriman (Amarphal)	<i>Monstera deliciosa</i> Liebm.	Araceae	Entire fruit (Berry)	"
Elephant apple or Wood apple (Karbel, Kavitha)	<i>Feronia limonia</i> (L.) Swingle	Rutaceae	Succulent placenta and inner pericarp of the fruit Amphisarca (Berry type)	"
Elephant apple (Chalta)	<i>Dillenia indica</i> L.	Dilleniaceae	Persistent fleshy sepals (Pseudocarp—false fruit)	"
Embelic (Amlaki, Amla)	<i>Embllica officinalis</i> Gaertn.	Euphorbiaceae	Entire fruit except seed (Berry)	"
Grape-fruit (Anjeer)	<i>Citrus paradisi</i> Macf.	Rutaceae	Juicy hairs developing from the inner wall of endocarp of the fruit (Hesperidium)	"
Grape-vine* or (Angur)	<i>Vitis vinifera</i> L.	Viaceae	Pericarp and placenta of the fruit (Berry)	"
Groundnut (Chinabadam, Mungphali)	<i>Arachis hypogaea</i> L.	Leguminosae (Papilionaceae)	Cotyledons (seeds) of the fruit (Lomentum)	"

COMMON NAME		BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS		MAIN USES
Guava (Peyara, Amrud)		<i>Psidium guajava</i> L.	Myrtaceae	Pericarp with thalamus fused (Berry)	Used as raw fruits	
Hog-plum (Amra, Ambara)		<i>Spondias pinnata</i> Kurz.	Anacardiaceae	Mesocarp of the fruit (Drupe)		"
Jack fruit (Kathal)		<i>Artocarpus heterophyllus</i> Lamk.	Moraceae	Fleshy perianth of the composite fruit (Sorosis)		"
Jujube (Kul, Boroj, Bar)		<i>Ziziphus mauritiana</i> Lamk.	Rhamnaceae	Epicarp and mesocarp of the fruit (Drupe)		"
Lemon (Pati, Goralebu, Bara-nimbu)		<i>Citrus limon</i> Burm. f.	Rutaceae	Juicy, unicellular hairs developing from the inner wall of endocarp of the fruit (Hesperidium)		"
Lime (Kagzi lebu)		<i>Citrus aurantifolia</i> Swing.	"	"		"
Litchi (Lichi, Lichu)		<i>Litchi chinensis</i> Sonn.	Sapindaceae	Fleshy aril of the fruit (one seeded modified berry)		"
Loquat (Loketphal, Lokat)		<i>Eriobotrya japonica</i> Lindl.	Rosaceae	Pericarp of the fruit		"
Lotus (Padma, Kamal)		<i>Nelumbo nucifera</i> Gaertn.	Nymphaeaceae	Thalamus and seeds of the fruit (Etaerio of achenes)		"
Mandarin orange (Kamala-lebu, Sautra)		<i>Citrus reticulata</i> Blanco	Rutaceae	Juicy unicellular hairs developing from the inner wall of endocarp of the fruit (Hesperidium)		"
Mango (Am, Aam, Ammra)		<i>Mangifera indica</i> L.	Anacardiaceae	Mesocarp of the fruit (Drupe)		"
Mangosteen (Bilati gab)		<i>Garcinia mangostana</i> L.	Guttiferae	Aril of the fruit (Berry)		"
Mulberry (Toot)		<i>Morus alba</i> L.	Moraceae	Perianth of the fruit (Sorosis)		"
Musk melon (Kharbuza, Phuti)		<i>Cucumis melo</i> L.	Cucurbitaceae	Mesocarp and endocarp of the fruit (Pepo)		"
Papaya (Peypey, Papita)		<i>Carica papaya</i> L.	Caricaceae	Pericarp of the fruit (Berry)		"
Peach (Aru)		<i>Prunus persica</i> Stokes	Rosaceae	Epicarp and mesocarp of the fruit (Drupe)		"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Pear (Nashpati, Nakh)	<i>Pyrus communis</i> L.	Rosaceae	Fleshy thalamus of the fruit (Pome)	Used as raw fruit
Persimmon or Kâki (Gab, Halwa tendu)	<i>Diospyros kaki</i> L. f.	Ebenaceae	Pericarp and fleshy thalamus (Berry)	"
Phalsa	<i>Grewia asiatica</i> L.	Tiliaceae	Succulent pericarp of the fruit (Berry)	"
Pineapple (Anaras, Ananas)	<i>Ananas comosus</i> Merr.	Bromeliaceae	Rachis, bract, perianth and pericarp fused together of the fruit (Sorosis)	"
Pistachio nut (Pista)	<i>Pistacia vera</i> L.	Anacardiaceae	Seed of the fruit (Nut)	"
Plum or Bullace (Alucha, Alu bokhara)	<i>Prunus domestica</i> L. subsp. <i>insitita</i> (L.) Schneid.	Rosaceae	Mesocarp of the fruit (Drupe)	"
Pomegranate (Anar, Bedana)	<i>Punica granatum</i> L.	Punicaceae	Succulent testa of the seed within fruit (Balausta-modified berry)	"
Raspberry	<i>Rubus lasiocarpus</i> Sm. and <i>R. idaeus</i> L.	Rosaceae	Pericarp of the fruit (Etaerio of Drupes)	"
Rose-apple (Gulab-jam)	<i>Syzygium jambos</i> (L.) Alston	Myrtaceae	Pericarp with thalamus fused of the fruit (Berry)	"
Sapodilla or Sapota (Sabeda)	<i>Achras zapota</i> L.	Sapotaceae	Mesocarp of the fruit (Berry)	"
Shaddock or Pummelo (Bata-bi lebu, Batavi nimbu)	<i>Citrus maxima</i> Merr.	Rutaceae	juicy, unicellular hairs developing from the inner wall of endocarp of the fruit (Hesperidium)	"
Strawberry	<i>Fragaria vesca</i> L.	Rosaceae	Fleshy thalamus of the fruit (Etaerio of achenes)	"
Sweet orange (Mozambic, Musambi, Malta)	<i>Citrus sinensis</i> Osbeck.	Rutaceae	juicy, unicellular hairs developing from the inner wall of endocarp of the fruit (Hesperidium)	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Tamarind (Tentul, Imli)	<i>Tamarindus indica</i> L.	Leguminosae (Caesalpiniace)	Mesocarp and endocarp of the fruit (Lomentum)	Used as raw fruit
Walnut (Ak hrot)	<i>Juglans regia</i> L.	Juglandaceae	Lobed cotyledons of the fruit (Drupe)	"
Water melon (Tarmooz, Tar- booz)	<i>Citrullus vulgaris</i> Schr. ex Eckl. & Zeyh.	Cucurbitaceae	Mesocarp and endocarp of the fruit (Pepo)	"
Water rose-apple (Jamrool)	<i>Syzygium aqueum</i> (B.f) Alston	Myrtaceae	Pericarp with thalamus fused of the fruit (Berry)	"
Wood-apple or Bael (Bel)	<i>Aegle marmelos</i> (L.) Corr.	Rutaceae	Succulent placenta and inner pericarp of the fruit (Amphisarca—modified berry)	"
V. Plants yielding Oils :				
A. Fatty oils :				
Black mustard (Benarasi rai, Kali sarson)	<i>Brassica nigra</i> Koach.	Cruciferae	Seeds	The oil, obtained from seeds, is used for cooking.
Brown mustard or Sarson (Sa- ristha, Sarson)	<i>B. campestris</i> L. var. <i>dicho-</i> <i>toma</i> Watt.	"	"	Oil obtained from seeds is used for cooking.
Candle nut (Jangli Akhrot)	<i>Aleurites moluccana</i> Willd.	Euphorbiaceae	"	Oil obtained from seeds is used in the manufac- ture of varnishes and paints.
Castor (Rehri)	<i>Ricinus communis</i> L.	Euphorbiaceae	"	Castor oil obtained from seeds is used as lubri- cant and as a purgative.
Clove (Laung, Labanga)	<i>Syzygium aromaticum</i> Merr. & Perry	Myrtaceae	Dried ovary of the flower	Oil is used medicinally and also as a clearing reagent in the biological laboratory.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY		MAIN USES
			IMPORTANT PARTS		
Coconut (Narikel) .	<i>Cocos nucifera</i> L.	Palmae	Dried meat (kernel) or Copra		Refined oil is used as cooking-oil, also used as hair-oil and as an illuminant.
Cotton seed (Tula bij)	<i>Gossypium arboreum</i> L., <i>G. herbaceum</i> L., <i>G. hirsutum</i> L. etc.	Malvaceae	Seeds		Pure refined oil is used as a salad and cooking oil and also for making oleomargarine.
Groundnut (Cheena baum, Mungphali)	<i>Arachis hypogaea</i> L.	Leguminosae	Seeds		Oil is used in the manufacture of hydrogenated fat, margarine, soap and toilet products.
Indian colza, Rapeseed or Yellow sarson (Sarisha, Sarson)	<i>Brassica campestris</i> L. var. <i>sarson</i> Prain	Cruciferae	"	}	Oil is used mainly as edible for cooking—also used as an illuminant.
Indian mustard (Rai sarisha, Rai)	<i>B. juncea</i> (L.) Czern. & Coss	"	"		
Indian rape (Toria, Tori sarisha)	<i>B. campestris</i> L. var. <i>toria</i> Duth.	"	"		
Linseed (Tishi, Alsi)	<i>Linum usitatissimum</i> L.	Linaceae	"		
Mahua	<i>Madhuca butyracea</i> (Roxb.) Mach.	Sapotaceae	"		Oil is used for the manufacture of margarine and soaps.
Niger seed (Ramtil, Sarguza)	<i>Guizotia abyssinica</i> Cass	Compositae	"		Refined oil is used as edible—also used as illuminants and for the manufacture of soaps.

COMMON NAME	BOTANICAL NAME	ECONOMICALLY IMPORTANT PARTS		MAIN Uses
		FAMILY		
Olive (Jalpai, Zaitum)	<i>Olea europaea</i> L.	Oleaceae	Fruits	Oil is used as salad and cooking oil, in canning and in medicine—also used as lubricants and for soap making.
Palm or oil Palm	<i>Elaeis guineensis</i> Jacq.	Palmæ	Fibrous pulp of the fruit	Oil is used for soap making and in the manufacture of tin plate,terne plate.
Perilla (Bhanjira, Bhasinda)	<i>Perilla frutescens</i> Britt.	Labiatae	Seeds	Oil is used in the manufacture of oil-p a p e r, water-proof clothes, printing-ink etc.
Rocket-salad or Roquette (Sweet sarisha, Taramira)	<i>Eruca sativa</i> Mill.	Cruciferae	"	Oil obtained from seeds is used for burning purposes.
Safflower (Kusum, Barre)	<i>Carthamus tinctorius</i> L.	Compositae	"	Oil is used for making soaps, paints, varnishes, linoleum etc.
Sesame (Til, Gingelly)	<i>Sesamum indicum</i> L.	Pedaliaceae	"	Oil is used as cooking oil, also used for anointing the body, in the manufacture of perfumery oils, soaps and cosmetics.
Soyabean (Gari kalai, Bhat)	<i>Glycine max</i> Merr.	Leguminosae	"	Refined soyabean oil can be used as cooking oil—also used for the manufacture of candles, soap, varnishes, lacquers, paints linoleum, etc.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Sunflower (Surjamukhi)	<i>Helianthus annuus</i> L.	Compositae	Seeds	Oil is used in medicine, in margarines and lard substitutes.
Tung-oil or China wood*	<i>Aleurites fordii</i> Hemsl.	Euphorbiaceae	Seeds	Oil is used in the soap and varnish industry as a substitute for linseed oil.

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Walnut	<i>Juglans regia</i> L.	Juglandaceae	Mature kernel of the fruit	Oil is used for artists' oil-paints, white-paints, soap and printing-ink.
White mustard (Sweet rai)	<i>Brassica hirsuta</i> Moench., <i>B. alba</i>	Cruciferae	Seeds	Like those of Indian mustard.
<i>B. Essential Oils :</i>				

Calamus (Bach)	<i>Acorus calamus</i> L.	Araceae	Rhizomes	Essential oil is used in perfumery.
Camphor (Karpur)	<i>Cinnamomum camphora</i> (L.) Nees & Eberm.	Lauraceae	Leaves	"
Cedarwood	<i>Juniperus macrocarpa</i> Boiss	Cupressaceae	Sowdust and shavings	Oil is used for linoleum.
Champa (Champa)	<i>Mitchella champaka</i> L.	Magnoliaceae	Flowers	Oil is used in perfumery.
Citronella (Kamather)	<i>Cymbopogon nardus</i> (L.) Rendle	Gramineae	Leaves	Oil is used in perfumery and cosmetics, also used in mosquito-repellent preparation.
Geranium	<i>Pelargonium capitatum</i> (L.) Ait.	Geraniaceae	Leaf shoots	Oil is used in soap and perfume industry.
Jasmine	<i>Jasminum auriculatum</i> Vahl.	Oleaceae	Flowers	Oil is used in the preparation of hair oils and attar.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Khus or Oil of Vetiver	<i>Vetiveria zizanioides</i> (L.) Nash	Gramineae	Roots	Oil is used in perfumery, soaps, cosmetics and for flavouring drinks.
Lavender	<i>Lavandula officinalis</i> Chaix	Labiatae	Flowers	Oil is used in perfumery
Lemon grass	<i>Cymbopogon flexuosus</i> (DC) Stapf, <i>C. citratus</i> (DC) Stapf	Gramineae	Leaves	Oil used in perfumery
Palmarose oil (Bujina)	<i>Cymbopogon martini</i> (Roxb.) Wats	Gramineae	Flowers and leaves	Oil is used in perfumery and cosmetics
Macassar or Ylang-ylang	<i>Cananga odorata</i> Hk. f. & Thom.	Annonaceae	Flower petals	"
Neroli	<i>Citrus aurantium</i> L.	Rutaceae	Flowers	"
Orange	<i>Citrus aurantium</i> L.	Rutaceae	Leaves and ripe peel of the fruit	Oil is used in confectionary, cosmetics and perfumery.
Rose oil, Otto of Roses (Gulab)	<i>Rosa damascena</i> Mill., <i>R. centifolia</i> L., <i>R. chinensis</i> Jacq.	Rosaceae	Flower petals	Essential oil (otto of roses) is used in perfumery and in making rose-water, attar etc.
Rosemary	<i>Rosmarinus officinalis</i> L.	Labiatae	Leaves and flowering tops	Used in making toilet-soap.
Sandal-wood (Sweet chandan)	<i>Santalum album</i> L.	Santalaceae	Wood	Oil is used in perfumery
Viola or Sweet violet (Bana-fsha)	<i>Viola odorata</i> L.	Violaceae	Flowers	"
VI. Plants yielding Fibres : Coir	<i>Cocos nucifera</i> L.	Palmae	Fibrous mesocarp of the fruit.	Coir (i.e. short and coarse fibres) is used for small cordage, brushes, bristles of doormats, sacks, and for stuffing purposes.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Cotton (Karfas, Kapas) Asiatic cotton or Levant Egyptian or Sea-island cotton	<i>Gossypium</i> spp. <i>G. herbaceum</i> L. <i>G. arboreum</i> L. var. <i>madam</i> Prokh. (Syn : <i>G. barbadense</i> L.)	Malvaceae	Seeds—the surface of which bears fibres	Fibres are used in the manufacture of textiles of all grades, rubber- tyre fabrics etc.
Tree cotton Upland cotton	<i>G. arboreum</i> L. <i>C. hirsutum</i> L.	}		
Blue Elephant Aloe (Kuwar- buti)	<i>Agave vera-cruz</i> Mill.			
Brown hemp, Mesta, Bimlipat- tam jute or Deccan hemp (Ambari, Patsan)	<i>Hibiscus cannabinus</i> L.	Malvaceae	Stem	Fibres are used for the manufacture of ropes, cordages and mats. Fibres are used for making ropes, cordage and paper-pulp.
Flax (Aisi)	<i>Linum usitatissimum</i> L.	Linaceae	Stem	Fibres are used for making linen cloth, twines and wrapping- papers.
Hemp (Ganja, Bhang)	<i>Cannabis sativa</i> L.	Cannabinaeae	Stem	Fibres are used for ropes, twines, carpets etc.
Henquen or Mexican sisal Indian mallow or China jute (Nahani khatpat)	<i>Agave fourcroydes</i> Lem. <i>Abutilon theophrasti</i> Medic.	Agavaceae Malvaceae	Leaves Stem	” ” Fibres are mainly used in rug-making.
Jute (Pat) Tossa jute or Jewsmallow (Mitha path) White jute (Titia pat)	<i>Cochorus</i> spp. <i>C. olitorius</i> L. <i>C. capsularis</i> L.	Tiliaceae	Stem	Fibres are used for rough weaving and coarse cloth, gunny bags, twine, carpets, covers for cotton bales etc.
Magney or Manlia magney	<i>Agave cantala</i> Roxb.	Agavaceae	Leaves	Fibres are used for the manufacture of twines, ropes, cordage etc.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Manila hemp or Abaca	<i>Musa textilis</i> Nees	Musaceae	Outer portion of leaf bases	Fibres are used for the manufacture of high- grade cordage, twine, bagging, paper-mache, tissue-paper, wrapping- paper etc.
Ramie (Kankhura)	<i>Boehmeria nivea</i> (L.) Gaud.	Urticaceae	Shoots	Used for sacks, threads, cordage, paper and gas- mantles.
Red silk-cotton (Simul tula)	<i>Bombax ceiba</i> L.	Bombacaceae	Inner wall of the fruit	Silky floss is used for stuffing purposes.
Roselle, Rama Jamaica sorrel	<i>Hibiscus sabdariffa</i> L.	Malvaceae	Stem	Fibre is used for mak- ing ropes and cordage.
Sunnhemp, San or Sunn (Shan, Patua)	<i>Crotalaria juncea</i> L.	Leguminosae (Papilionaceae)	Stem	Used for making ropes, mats, cordage, paper etc.
Sisal hemp or Agave (Konga, Sisal, Sann)	<i>Agave sisalana</i> Perr.	Agavaceae	Leaves	Used for the manufac- ture of ropes.
VII. Plants yielding Beverages :				
Coffee (Kafi)	<i>Coffea arabica</i> L.	Rubiaceae	Seeds	Used as beverage
Cocoa or Cacao (Koko)	<i>Theobroma cacao</i> L.	Sterculiaceae	Seeds	"
Tea (Cha, Chale)	<i>Camellia sinensis</i> (L.) O. Ktze.	Ternstroemiaceae	Tender leaves	"
VIII. Plants yielding Sugars and Starch :				
Palm sugar	<i>Borassus flabellifer</i> L. <i>Phoenix sylvestris</i> Roxb. }	Palmac	Shoot tips	Young shoot tips after tapping yield a sugary juice known as toddy —used for making sugar, gur and alcohol.
Shoiti food	<i>Curcuma zedoaria</i> Rosc.	Zingiberaceae	Underground stem (tubers)	The shoot starch of com- merce is the product extracted from the tu- bers and used as a substitute for arrow- root and barley.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Sugar beet	<i>Beta vulgaris</i> L. var. <i>rapa</i> Dum.	Chenopodiaceae	Roots (Napiform)	Sweet sap is used for making sugar.
Sugarcane (Akh, Ganna)	<i>Saccharum officinarum</i> L.	Gramineae	Stems	"
Sugar maple	<i>Acer saccharum</i> Marshall	Aceraceae	Stems	"
Tapioca (Shimul alu, Ganna, Naisbakar)	<i>Manihot esculenta</i> Crantz. <i>M. utilissima</i> Pohl.	Euphorbiaceae	Stems and roots (tubers)	Roots and Stems are used as starchy food.
IX. Plants yielding Narcotics and Masticatories :				
Betel nut (Supari)	<i>Areca catechu</i> L.	Palmae	Seeds	Seeds i.e. nuts are chewed along with betel leaves and also as spices.
Indian hemp or Hemp (Ganja, Bhang, Charas)	<i>Cannabis sativa</i> L.	Cannabinaceae		For <i>ganja</i> —female inflorescence coated with resinous exudation. For <i>bhanga</i> —dried flowering shoots and leaves of both male and female plants.
Poppy or Opium (Afinq, Posio, Post)	<i>Papaver somniferum</i> L.	Papaveraceae	Latex of the immature fruits.	Used to induce sleep, relieve pain and relax spasms.
Tobacco (Tamak, Tambaku)	<i>Nicotiana tabacum</i> L.	Solanaceae	Leaves	Used for smoking, chewing, snuff etc.
X. Plants yielding Rubber : Assam or India rubber (Bor)	<i>Ficus elastica</i> Roxb.	Moraceae		Latex obtained from the bark of the stem and branches.
Ceara or Manicoba rubber	<i>Manihot glaziovii</i> Muell.-Arg.	Euphorbiaceae		Latex from the bark of the stem and roots.
Dandelion rubber	<i>Taraxacum officinalis</i> Weber	Compositae	Latex from long tap roots	"

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Guayule rubber	<i>Parthenium argentatum</i>	Compositae	Scattered granules of caoutchouc present; all through the tissues.	Used for mixing with synthetic rubber substitutes.
Panama or Castilla rubber	<i>Castilleja elastica</i> Cerv.	Moraceae	Latex from the bark of the stem	Used for making rubber-goods.
Para rubber or Hevea rubber (Rabar, Rubber)	<i>Hevea brasiliensis</i> (HB. & K) Muell.-Arg	Euphorbiaceae	"	This good quality rubber is used for the manufacture of top grade rubber goods like tyres and tubes, water-proof clothings, cushions, shoes and boots, insulated wires, toys etc.
XI. Timber-yielding Plants :				
Basswood or Linden	<i>Tilia americana</i> L.	Tiliaceae	Wood	Used for making boxes, crates, wooden ware, furniture, plywood, picture frames etc.
Boxwood	<i>Gossypiospermum praecox</i> Urb. (= <i>Casuarina praecox</i> Griseb.)	Flacourtiaceae	"	Used for the manufacture of engraver's blocks, rulers, scientific and musical instruments, veneers etc.
Cedrela tree or Red Cedar (Toon)	<i>Toona ciliata</i> Roem.	Meliaceae	"	Used for furniture, door panels, carvings, for making tea-boxes, cigar-boxes etc.
Deodar or Himalayan Cedar (Daru)	<i>Cedrus deodara</i> Loud.	Pinaceae	"	Mainly used for railway sleepers, bridge-work, beams, door and window frames etc.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY	
			IMPORTANT PARTS	MAIN USES
Ebony (Ebnaa, Ablus)*	<i>Diospyros ebenum</i> Koenig.	Ebenaceae	Wood	Wood is used for cabinet work, rulers, chopsticks, pipes etc.
Elm (Maral)	<i>Ulmus wallichiana</i> Planch.	Ulmaceae	"	"
Gurjun	<i>Dipterocarpus indicus</i> Bedd., <i>D. turbinatus</i> Gaertn. f.	Dipterocarpaceae	"	Used for building purposes.
Hemlock	<i>Tsuga canadensis</i> Carr.	Pinaceae	"	" " shingles.
Indian rosewood (Shisham, Sissu)	<i>Dalbergia latifolia</i> Roxb.	Papilionaceae	"	Used mainly for furnitures, also used for agricultural implements, cart-wheels etc.
Laurelwood or Indian laurel (Surpan)	<i>Calophyllum inophyllum</i> L.	Guttiferae	"	Used for constructional purposes, furniture, packing-cases, plywoods, veneers etc.
Lebbeck or Parrot tree (Siris)	<i>Albizia lebbeck</i> (L.) Benth.	Mimosae	"	Used for railway-carriages, furniture, structural work and interior fittings.
Mahogany	<i>Swietenia mahagoni</i> (L.) Jacq.	Meliaceae	"	Wood is used for making boats, carts and carriages, agricultural implements, in construction and for furniture.
Oak	<i>Quercus dilatata</i> Lindl.	Fagaceae	"	Used for construction work and agricultural implements.
Padouk or Andaman redwood	<i>Pterocarpus indicus</i> Willd.	Papilionaceae	"	Used for furniture, cabinet work, turnery and veneers.
Pinewood	<i>Pinus</i> spp.	Pinaceae	"	Wood is used for construction work, railway-sleepers, packing cases, pencils, pen holders, match-boxes etc.
Queen crape-myrtle (Jarul)	<i>Lagerstroemia speciosa</i> (L.) Pers.	Lythraceae	"	The wood is used for structural work, flooring etc.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY	
			IMPORTANT PARTS	MAIN USES
Red Sandalwood (Lal chandan)	<i>Pterocarpus santalinus</i> L. f.	Papilionaceae	Wood	Wood is used for construction work—also used for dyeing cloth, wood and leather.
Sal	<i>Shorea robusta</i> Gaertn. f.	Dipterocarpaceae	"	Wood is used for piles beams, planking and railing of bridges, railway-sleepers, canoes, window and door-frames, etc.
Sissoo (Shisham, Sissu)	<i>Dalbergia sissoo</i> Roxb.	Papilionaceae	"	Like Indian rosewood.
Sainwood (Bhirra)	<i>Chloroxylon swietenia</i> DC.	Rutaceae	"	Used for cabinet work and furniture.
Teak (Sagoon)	<i>Tectona grandis</i> L. f.	Verbenaceae	"	Mainly used for house and ship building, for bridges, railway sleepers, furnitures, shingles, etc.
White Sandalwood (Sweet chandan)	<i>Santalum album</i> L.	Santalaceae	"	Wood is used for making boxes and other small articles which are beautifully carved.
XII. Common drug-yielding Plants :				
Akund (Sweet akanda, Safed-ak)	<i>Calotropis procera</i> R. Br.	Asclepiadaceae	Leaves, bark of the root and latex	Leaves are used for relieving pain in rheumatism. Latex is used in curing piles, ring worm etc. The bark is used in the treatment of skin diseases.
Ammi, Lovage (Joan, Ajiowan)	<i>Trachospermum ammi</i> (L.) Sprague	Umbelliferae	Fruits	Used as carminative, stimulant, tonic and in indigestion.
Asiatic pennywort (Thankuni, Brahmi)	<i>Centella asiatica</i> (L.) Urban	"	Leaves	Decoction of leaves is taken in diarrhoea and dysentery.
Black cutch (Khayer, Katha)	<i>Acacia catechu</i> (L. f.) Willd.	Mimosae	Gum	Used in the treatment of tooth decay.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Brahmi	<i>Herpestis monieria</i> H. B. & K.	Scrophulariaceae	Leaves	Leaf-decoction is used as a nerve-tonic, also in epilepsy and insanity.
Castor (Rehri, Rendi)	<i>Ricinus communis</i> L.	Euphorbiaceae	Oil extracted from seeds	Used as purgative, also used in chronic rheumatism.
Chaulmogra (Chalmugra)	<i>Taraktogenos kurzii</i> King	Flacourtiaceae	“ “	Used in the treatment of leprosy and skin diseases.
Chinese Chaste tree (Nishinda, Nirgandi)	<i>Vitex negundo</i> L.	Verbenaceae	Root and leaves	Used as a tonic and a febrifuge and also as a diuretic. Leaves are used in curing rheumatism.
Chiretta (Chirata, Kiryat-charayatah)	<i>Sweria chirata</i> Buch-Ham.	Gentianaceae	Stem	Used as a tonic, stomachic and laxative.
Cinchona (Sinkona, Quinine)	<i>Cinchona calisaya</i> Wedd. C. } <i>ledgeriana</i> Moens ex Trimen } <i>C. succirubra</i> Pav. ex Klotz. }	Rubiaceae	Bark	Alkaloids obtained from barks are used as a tonic and in the treatment of malarial fevers.
Cotton abroma (Ulatkambal, Kumal)	<i>Abronia angusta</i> L. f.	Sterculiaceae	Bark of the plant	Used in dysmenorrhoea.
Country mallow or Indian aboution (Potari, Kanghi)	<i>Abutilon indicum</i> G. Don	Malvaceae	Seeds	Used in the treatment of leucoderma.
Crear (Kalmegh, Kiryat)	<i>Andrographis paniculata</i> (Burm. f.) Wall. ex Nees	Acanthaceae	Root and Leaves	Root is stomachic, leaf decoction is used as a liver tonic—also useful in diarrhoea, flatulence etc.
Croton (Joypal, Jamalgota)	<i>Croton tiglium</i> L.	Euphorbiaceae	Seeds	Oil obtained from seeds is used as a strong purgative.
Deadly nightshade or Belladonna (Yebriji, Sag angur)	<i>Atropa belladonna</i> L.	Solanaceae	Leaves, shoots and roots	Atropine, obtained from dried leaves is used to dilate the pupil of the eye. The drug belladonna obtained from dried leaves, shoots and roots is used to relieve pain, cough and excessive perspiration.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Devil or Dita bark tree (Chaitum, Chaitum) Digitalis, Forglove	<i>Astonia scholaris</i> (L.) R. Br. <i>Digitalis purpurea</i> L.	Apocynaceae Scrophulariaceae	Bark Leaves	It is used in convalescence, fever, debility etc. It is used as cardiac stimulant and tonic.
Easter tree (Kurchi)	<i>Holarthena antidysematica</i> Wall.	Apocynaceae	Seeds, leaves and barks of the stem	It is used in diarrhoea and dysentery.
Eucalyptus tree or Tasmanian blue gum	<i>Eucalyptus globosus</i> Labill.	Myrtaceae	Leaves	Oil, obtained from dried lea- ves, is used in the treatment of nose, throat disorders, asthma, bronchitis etc.
Garlic (Rasun, Lashun)	<i>Allium cepa</i> L.	Liliaceae (Alliaceae)	Bulb	The juice of the bulb is used in fever, dropsy, ear-ache, skin diseases and also for relieving pain caused by insect bites.
Horse purslane (Santhi, Lalsa- buni)	<i>Trianthema portulacastrum</i> L.	Aizoaceae	Entire plant	Decoction of the plant is used in curing beri-beri.
Indian sarsaparilla (Ananta- mul, Salsa or Magrabu)	<i>Hemidesmus indicus</i> R. Br.	Asclepiadaceae	Root	It is used in dyspepsia, fever and skin diseases.
Ipecac	<i>Cephaelis ipecacuanha</i> (Brot.) Rich.	Rubiaceae	Root	It is used in dysentery, diar- rhoea—as an expectorant, it is used in chronic bronchitis, asthma, phthisis.
Kantkari, Katei	<i>Solanum xanthocarpum</i> Schrad. & Wendl.	Solanaceae	Root	The plant is used as febrifuge and as a antidote of small-pox.
Liquorice (Jastimodhu, Mul- hatti)	<i>Glycerhiza glabra</i> L.	Papilionaceae	Root	Root is used as a laxative, also in the treatment of sore throat.
Malabar nut (Basak, Adulasa)	<i>Adiantoda vasica</i> Nees	Acanthaceae	Leaves	It is used as an expectorant and relieves cough

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Margosa tree (Neem, Nim)	<i>Azadirachta indica</i> A. Juss	Meliaceae	Leaves, bark	It is used in the treatment of skin diseases.
Monk's hood (Kalbish, Miha zahar)	<i>Aconitum napellus</i> L.	Ranunculaceae	Root	Used in rheumatism, neuralgia and as a febrifuge.
Nux-vomica (Noxbumica, Kuchla)	<i>Strychnos nux-vomica</i> L.	Loganiaceae	Seeds	Used as a tonic, stimulant and in the treatment of paralysis and nervous disorders.
Opium, Poppy (Afing, Post)	<i>Papaver somniferum</i> L.	Papaveraceae	Fruits	Latex of the fruit is used to induce sleep, relieve pain and relax spasms.
Pig weed (Punarnaba, Thikri)	<i>Boerhaavia repens</i> L.	Nyctaginaceae	Roots	It is diuretic, laxative and anthelmintic.
Pine apple (Anaras, Ananas)	<i>Ananas comosus</i> (L.) Merr.	Bromeliaceae	Leaves	Juice of the leaves is used in gastric irritability, jaundice etc.
Prickly chaff-flower (Apang, Chichiri)	<i>Aerva aspera</i> Spreng.	Amaranthaceae	Seeds, roots	Used in the treatment of sores and boils.
Rauwolfia (Sarpagandha, Chotachand, Chandra)	<i>Rauwolfia serpentina</i> (L.)	Apocynaceae	Roots	Mainly used in the treatment of mental disorders, hypertension, in lowering high blood pressure etc.
Sweet flag (Bach, Safed bach)	<i>Acorus calamus</i> L.	Araceae	Stem	Used in lowering blood pressure and respiratory rate.
Thorn apple (Dhutura)	<i>Datura metel</i> L.	Solanaceae	Roots	Used in the treatment of asthma.
Wood apple or Bael (Bel, Bilva)	<i>Aegle marmelos</i> (L.) Corr.	Rutaceae	Bark of the root	It is used in intermittent fever, heart trouble etc.
Worm seed, Santonine	<i>Artemisia absinthium</i> L. and <i>A. maritima</i> L.	Compositae	Unopened flower	It is used as vermifuge, stimulant and tonic.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
XIII. Plants yielding Condiments and Spices :				
Ajmund, Radhuni	<i>Apium graveolens</i> Roxb.	Umbelliferae	Seeds	Used as spice in Indian cookery.
Anise (Mahuri, Saunf, Saouf)	<i>Pimpinella anisum</i> L.	Umbelliferae	Dried ripe fruits	Used as spices, also used in medicine for its carminative and expectorant properties.
Aromatic cardamom (Moranga elach, Chouli elachy)	<i>Amomum aromaticum</i> Roxb.	Zingiberaceae	Dried seeds	Used as spices, and as an ingredient with betel leaf.
Asafoetida (Hing, Hingra)	<i>Ferula foetida</i> Regel., <i>F. allicia</i> Boiss., <i>F. narthex</i> Boiss.	Umbelliferae	Gum resins of the root	Used as a condiment in many preparations of Indian cookery.
Betel-nut, Areca-nut (Supari)	<i>Areca catechu</i> L.	Palmae	Seed together with endosperm	Chewed as a masticator with betel leaves
Betel-vine (Pan, Paan)	<i>Piper betle</i> L.	Piperaceae	Leaves	Betel leaves are chewed raw, leaves are also used as paul- tice for various complaints.
Bishop's weed (Joan, Ajowan)	<i>Trachyspermum ammi</i> (L.) Sprague	Umbelliferae	Seeds	Used as a spice or condiment, sometimes used with betel leaf for chewing.
Black cummin (Kalojira, Kalonji)	<i>Nigella sativa</i> L.	Ranunculaceae	Seeds	Used as a spice in curries and other dishes.
Black mustard (Benarasi rai sarisha, Kalisarsoon, Asli rai)	<i>Brassica nigra</i> (L.) Koch	Cruciferae	Seeds	Powdered seeds mixed with a little starch and water is used as table-mustard.
Black pepper (Gol morich, Kali mirich)	<i>Piper nigrum</i> L.	Piperaceae	Small one-seeded fruits (berries)	Pepper is one of the most valuable of spices. It is used in the preparation of sauces, soups, curries etc.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS	MAIN USES
Caraway (Jira, Shia-jira)	<i>Carum curvi</i> L.	Umbelliferae	Seeds	Used as a spice for culinary purpose and for flavouring bread, cakes and cheese ; also used in the manufacture of Kummel and as an ingredient of sausage.
Cassia lignea or Indian cassia bark, leaves (Teipata)	<i>Cinnamomum tamala</i> Nees.	Lauraceae	Leaves	Leaves are used as a spice in curry dishes, especially as a flavouring agent.
Chilli, Goat pepper, Spur pepper (Lanka, Lal mirich)	<i>Capiscum frutescens</i> L.	Solanaceae	Fruits	Eaten raw or cooked as spice as principal ingredient in all chutneys and curing process, also used for flavouring pickles.
Coriander (Dhane, Dhania)	<i>Coriandrum sativum</i> L.	Umbelliferae	Young leaves and mature seeds	Young leaves are used in salads and for flavouring soups. The seeds are extensively used as spice in confectionaries.
Cumin (Jira, Jeera)	<i>Cuminum cyminum</i> L.	Umbelliferae	Fruits	Used as an indispensable spice in almost all curry preparations. Fruits are often candied, may be used externally as poultice.
Cutch tree (Khayer, Khair)	<i>Acacia catechu</i> Willd.	Leguminosae (Mimosae)	The resinous extract obtained by boiling the chips of heartwood yields <i>cutch</i> and <i>kath</i> .	Kath is used for chewing with betel leaves and also as a medium for cine white cutch is used for tanning and dying purposes.
Fennel (Mouri, Pan mouri, Sour, Saunt)	<i>Foeniculum vulgare</i> Mill.	Umbelliferae	Young leaves, seeds and fruits	Young leaves are used as a flavouring agent, either raw or cooked with curry. Seeds are also used for flavouring and are distilled for the oil. Fruits are used as a masticatory.

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY IMPORTANT PARTS		MAIN USES
Fenugreek (Methi, Maythi)	<i>Trigonella foenum-graecum</i> L.	Leguminosae	Seeds	Seeds are used extensively in cookery as a condiment or spice.	
Garlic (Rashun, Lahsoon)	<i>Allium sativum</i> L.	Liliaceae (Alliaceae)	Bulb (stem)	Used in salads and for flavouring rich dishes as spice.	
Ginger (Ada, Adrakh)	<i>Zingiber officinale</i> Rosc.	Zingiberaceae	Rhizome (stem)	Ginger is used as a spice in cookery and medicine.	
Indian mustard, Mustard (Rai sarisha, Asi Rai, Raie)	<i>Brassica juncea</i> Coss.	Cruciferae	Seeds	The seeds (broken, pasted or unbroken) are used to flavour curries.	
Large cardamom (Bara clach, Bara liaichy)	<i>Amomum subulatum</i> Roxb.	Zingiberaceae	Seeds	Highly aromatic seeds form an ingredient with betel leaf; seeds are also used in the preparation of sweet-meats, also as an adjunct to other stimulants.	
Long pepper, The Cubebs (Pipul, Pipili, Mirch)	<i>Piper longum</i> L.	Piperaceae	Dried unripe fruits and roots.	Used as a spice; also used in medicine.	
Mint (Pudina, Pudena)	<i>Mentha piperita</i> L.	Labiatae	Leaves	Leaves are used for culinary and confectionary purposes.	
Nutmeg (Jaiphal, Jaitiri)	<i>Myristica fragrans</i> Houtt.	Myristicaceae	Hard brown oval kernel of the seed	Nutmegs are used medicinally and as a culinary spice. Grated nutmeg is used with pudding, custard, and other sweet dishes and with various beverages.	
Onion (Piaj, Piani)	<i>Allium cepa</i> L.	Liliaceae (Alliaceae)	Bulb together with fleshy leaf bases	Used as vegetables; and also as a flavouring reagent and spice in the preparation of rich dishes.	

COMMON NAME	BOTANICAL NAME	FAMILY	ECONOMICALLY	
			IMPORTANT PARTS	MAIN USES
Saffron (Jafraan, Saffron),	<i>Crocus sativus</i> L.	Iridaceae	Stigmas of the flower	Saffron is used mainly for colouring and flavouring butter, cheese, pudding, pasty confectionary and rich Indian dishes.
Sweet flag (Bach)	<i>Acorus calamus</i> L.	Araceae	Rhizomes (stem)	Used in the preparation of aromatic vinegar. In Europe, used as a spice for flavouring beer.
The clove (Lavanga, Long)	<i>Syzygium aromaticum</i> (L.) Merr.	Myrtaceae	Dried and unexpanded flower buds	Used as a spice in all rich preparations of Indian cookery; also chewed as a masticator with betel-nuts, betel-leaves etc.
The mango ginger (Amada, Amhalidi)	<i>Curcuma amada</i> Roxb.	Zingiberaceae	Rhizome (stem)	Used as condiment in the preparation of 'chutnies'.
True cardamom (Choto elach, Elaichi)	<i>Elettaria cardamomum</i> Maton.	Zingiberaceae	Ripe fruits containing seeds	Used as spice for flavouring dishes, also used as confectionary and as an ingredient in curry powder.
True cinnamon (Darchini, Datchini)	<i>Cinnamomum zeylanicum</i> Bl.	Lauraceae	Bark of the stem	Used as popular spice for flavouring food.
Turmeric (Halud, Haldi)	<i>Curcuma longa</i> L., <i>C. domestica</i> Val.	Zingiberaceae	Rhizome (stem)	It is used as an important spice and condiment in Indian cooking.
White mustard (Sweet rai, Benarasi rale)	<i>Brassica hirta</i> Moench, <i>B. alba</i>	Cruciferae	Seeds	The seeds as well as oil are used in Indian cookery.

SELECTED QUESTIONS

1. Mention the important economic food² plants of West Bengal. Describe briefly the method of cultivation of *any one* of them.
Refer Chapter 1. (Food Plants under the Classification of Economically Important Plants) and for cultivation refer article 2.1
2. Give the botanical names of the following plants, assign them to their respective families, mention their economic importance, the part used and conditions under which they grow best :—
(a) Gram, (b) Mustard, (c) Jute, (d) Sal
Refer articles 3.1 for (a) ; 12.4 for (b) ; 9.2 for (c) and 10.2 for (d)
3. Name the families to which any three of the following plants belong. Indicate why you refer them to these families and state the scientific names of the plants selected :
(a) Rice, (b) Coconut, (c) Radish, (d) Jute and (e) Mango,
Refer articles 2.1 for (a) ; 12.5 for (b) 4.1 for (c) ; 9.2 for (d) and 5.2 for (e).
4. Describe the botanical features of any one of the following crop plants and give a brief account of its method of cultivation.
Paddy, Jute and Sugarcane
Refer articles 2.1, 9.2 and 13.1 respectively.
5. Give the botanical names, the families to which they belong, their usefulness and the parts of the plants from which they are obtained of any five of the following :—
(a) Quinine, (b) Cotton, (c) Teak, (d) Groundnut, (e) Mustard oil, (f) Tea and (g) Mung.
Refer articles 7.3 for (a), 9.1 for (b), 10.1 for (c), 12.3 for (d), 12.4 for (e), 6.1 for (f) and 3.2 for (g)
6. Give the botanical name of rice plant. Describe different types of cultivation of rice in West Bengal. Can you suggest any improvement in our methods of rice cultivation ?
Refer article 2.1
7. Mention the botanical names of two plants from each of the following categories. Assign each to its family :—
(a) Oil-yielding, (b) Fibre-yielding, (c) Timber-yielding.
Select any one plant from your list and describe the method of cultivation of the same.
Refer the list of Economically Important Plants, Item nos, V, VI, XI ; for cultivation see articles 12.4 for (a), 9.2 for (b) and 10.1 for (c)
8. Mention the principal fibre-yielding plants of West Bengal and give their Latin names. Assign them to their respective families and indicate the plant parts from which the products are obtained.
Refer the list of Economically Important Plants, Item no. VI.
9. Refer any five of the following plants to their respective families and write short notes on their economic importance mentioning the parts used :
(i) *Cinchona officinalis* ; (ii) *Saccharum officinarum* ; (iii) *Thea sinensis* ;
(iv) *Corchorus olitorius* ; (v) *Triticum sativum*, (vi) *Rauwolfia serpentina* ;
(vii) *Brassica juncea* and (viii) *Cocos nucifera*.
Refer articles 7.3 for (i) ; 13.1 for (ii) ; 6.1 for (iii) ; 9.2 for (iv) ; 2.2 for (v) ; 7.2 for (vi) ; 12.4 for (vii) and 12.5 for (viii).

10. Enumerate the principal sugar-yielding plants and assign them to their families. Give an account of the process of extraction of sugar from sugar-beet.

Refer the list of Economically Important Plants, Item no. VIII and article 13.2

11. Give an account of the method of Jute cultivation in West Bengal.
Refer article 9.2

12. Why are the species of the following genera cultivated ? (a) *Psychotria*, (b) *Ricinus*, (c) *Lagerstroemia*, (d) *Saccharum*, (e) *Borassus* and (f) *Phaseolus*.

Refer the list of Economically Important Plants, Item no. XII for (a) ; V for (b) ; XI for (c) ; VIII for (d) and (e) ; II & III for (f).

13. (a) What are the useful parts of a coconut plant ? (b) What are the parts that yield the cotton of commerce ? (c) From where is quinine extracted ?

Refer the list of Economically Important Plants, Item nos. V & VI for (a) ; VI for (b) ; XII for (c).

14. What are the principal fibre-yielding plants of India ? Give an account of the cultivation of two important fibre-yielding plants of India.

Refer the list of Economically Important Plants, Item no. VI and articles 9.1 & 9.2.

15. Give a short account of the methods of tea and sugarcane cultivation in India.

Refer article 6.1 and 13.1

16. State reasons for which the following plants are cultivated. Mention the families to which each of the following belongs—

(a) *Rauvolfia serpentina*, (b) *Tectona grandis*, (c) *Triticum vulgare*, (d) *Arachis hypogaea*, (e) *Cinchona ledgeriana*.

Refer list of the Economically Important Plants, Item nos. XII for (a) ; XI for (b) ; I for (c) ; V for (d) ; and XII for (e)

17. Mention the name of species, the families to which they belong and the plant parts which yield (a) Sugar, (b) Jute, (c) Cotton, (d) Emetine and (e) Mustard oil.

Refer the list of Economically Important Plants, Item nos. VII for (a) ; VI for (b) and (c) ; XII for (d) and V for (e).

18. What is the species that yield tea of commerce ? Give an account of its method of cultivation and distribution in India.

Refer article 6.1

19. Write short notes on :—(a) Atropine, (b) Emetine, (c) Santonine, (d) Nicotine, (e) Menthol-yielding plants. Describe chief distinguishing characters of each of those families and general distribution of those plants in India.

Refer articles 7.4 (d) for a ; 7.1 for b ; 7.4 (p) for c ; 8.1 for d. Menthol-yielding plants are *Mentha arvensis* DC. var *piperascens* Holms. (Fam. Labiatae)—cultivated in Jammu and Kashmir. The leaves yield an essential oil which is the chief source of menthol. Other menthol-yielding plants are *Mentha piperita* L. (Labiatae)—cultivated in the Punjab, Kashmir and Maharashtra ; *M. longifolia* (L.) Huds (Labiatae)—cultivated in Kashmir, Punjab, Maharashtra and Menthol is used in the treatment of colds, also used as carminative, stimulant and for allaying nausea.

20. Write an essay on the cultivation of wheat and mustard. Discuss the methods by which yield of these two crops may be increased in West Bengal.

Refer articles 2.2 and 12.4 respectively.

21. Give the botanical name of the important rubber-yielding plants and mention the families to which they belong. Describe the methods of tapping of para rubber.

Refer the list of Economically Important Plants, Item no. X and article 11.1 (para rubber) for tapping.

22. Describe briefly the tobacco plant and general methods of its cultivation in Bengal. Discuss its commercial position in West Bengal after the partition.

Refer article 8.1

23. Describe the methods of cultivation of cotton-yielding plants in India. Give distinguishing characters of the silk-cotton tree and mention its economic importance.

Refer article 9.1 and for silk-cotton tree refer the list of Economically Important Plants, Item no. VI.

24. Name few important timber-yielding plants of India and assign them to the families to which they belong. Give a concise account of the minor forest products of India.

Refer the list of Economically Important Plants, Item no. XI and forest products refer chapter 10 (last para).

25. Write notes on :—

(a) Daturin, (b) Abromine, (c) Digitalis, (d) Quinine, (e) Ephedrine, (f) Atropine, (g) Morphine, (h) Lavenders.

For (a), (b), (c), (f)—refer article 7.4

For (d) refer article 7.3

(g) Morphine is an alkaloid obtained from the plant *Papaver somniferum* L. Refer article 7.4 (0).

(h) Lavender is obtained from *Lavandula officinalis* Chaix belonging to the family Labiatae. In India, it is grown in Jammu and Kashmir. Flowers contain an essential oil which is used in perfumery.

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**CYTOLOGY, GENETICS AND PLANT
BREEDING**

CHAPTER 1

The Cell

The body of the living organisms like plants and animals is composed of cells. The study of the cellular organism and its components particularly in relation to the functional organization of protoplasm comes under the special branch of biology (botany and zoology) called *cytology*. It is, therefore, the relation of the different organization of the cell with the phenomena of metabolism.

The transmission of parental qualities, expressed or latent to the offspring is called *heredity*. *Genetics* means genesis or origination of organisms. It is therefore the "elucidation of the phenomena of heredity and variation." So, the phenomena of heredity and variation comes under genetics. Genetics deals with all aspects of biology—with physiology, biochemistry, growth and development and many others.

1.1 The Cell and its Component parts : The word "cell" was first coined by the English scientist Robert Hooke in 1665 to designate the tiny structures present in a piece of cork. However, the enunciation of the *cell doctrine*, the basic aspects of which hold good even today, goes to the credit of two German scientists Schleiden (1838) and Schwann (1839). In modern terms the cell may be defined as *the basic structural and functional unit of a living organism and is the common denominator of a living body*.

With the gradual advancement of science and availability of improved tools and techniques of analysis, the concept of a cell has been vastly elaborated. In 1920, the main part of a cell was differentiated into **nucleus** and **cytoplasm**. Both the nucleus and cytoplasm are surrounded by their individual membranes, the nucleus by the **nuclear membrane** and the cytoplasm by the cell or **plasma membrane**. The cytoplasm which lies towards the outer periphery of the cell is termed as **ectoplasm**, whereas the cytoplasm in the inner portion is called the **endoplasm**. Cytoplasm has got several **vacuoles** within it. Besides these, the plant cell has a distinct rigid outer boundary known as **cell wall**. With the discovery of electron microscope and phase contrast microscope, the concept of a cell has been completely changed and has opened up a new domain to the cytologists and cell biologists.

CYTOPLASMIC ORGANELLES

When seen under a microscope the nucleus is seen as a well stained body in the cell. The cells in bacteria and blue-green algae are less organised than other plant and animal cells. The nucleus is

enveloped by a nuclear envelope. Within the nucleus a much organised nucleolus is present and a chromatin network. Between the nucleolus and chromatin network is the nucleoplasm.

Scattered within the cytoplasm, the following cytoplasmic bodies can be seen. (For detail refer Chapter 3, articles 3.1 and 3.3, in *Plant Physiology* portion).

(i) *Mitochondria*—These are the most important cytoplasmic organelles. They appear as rod-like or filamentous structures under the microscope. Within the mitochondria inter-membranes are present and which make compartments within the mitochondria.

(ii) *Endoplasmic reticulum*—It is the most extensive membrane network distributed throughout the cytoplasm. They are not visible under light microscope.

(iii) *Ribosomes*—These are the smallest recoverable bodies associated with membranes of the endoplasmic reticulum. These are recognised as tiny round particles and chemically contain ribonucleo-protein.

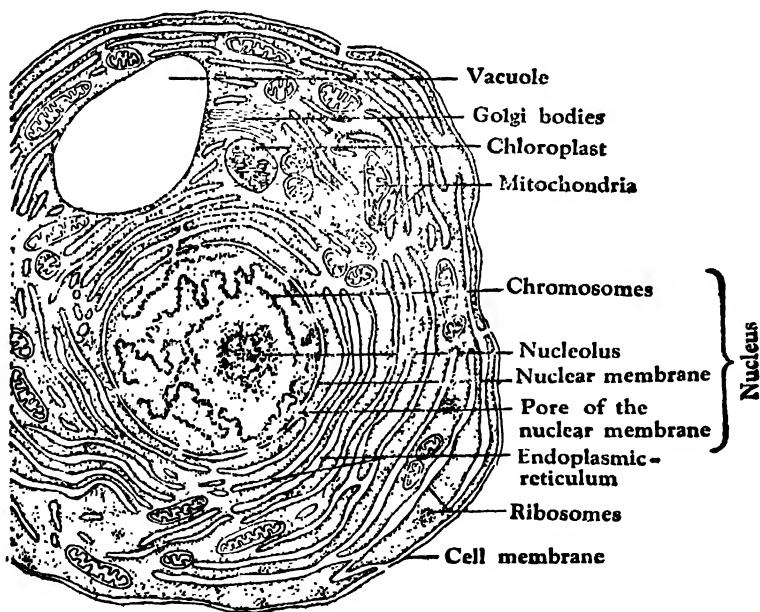


Fig. 1.1 An enlarged generalized cell, as seen with an electron microscope showing the various structures within it

(iv) *Golgi bodies*—They are limited in their distribution. Not regularly found in the cytoplasm of all cells. The golgi material

appears as reticulate or fibre-like under light microscope in some cell types.

(v) *Plastids*—The largest cytoplasmic organelles in plant cells are the plastids. Plastids have various shapes but are usually round, small, granular, discoid; rod-like plastids are also of frequent occurrence. Plastids are often coloured.

Plastids are of principally three kinds and these are as follows :

(a) *Leucoplasts* or colourless plastids are found in the food storage cell of stems, roots etc. where sunlight cannot reach.

(b) *Chloroplasts* or green plastids are found in algae and leaves and stems of higher plants.

(c) *Chromoplasts* or other than green-coloured plastids are found in the skin of fruits, petal of flowers, carrot etc.

1.2 Physical Properties of Cytoplasm : The physical properties of cytoplasm, basically the *hyaloplasm*¹, is a complex colloidal system. It contains a high percentage of water and many particles of varying sizes. Some of the materials are found in dissolved condition, but many of them are suspended in solution like oils and fats and many proteins.

The plant cell also contains droplets of fat, grains of starch and pigments. There are vacuoles which contain different kinds of substances. Within the vacuole, the so called cell sap is present and which consists of sugars, salts and anthocyanin pigments. The cytoplasm is separated from the vacuole by means of a membrane.

The physical properties of the *hyaloplasm* are jelly like i.e. it is in a gel phase. A gel is a group of suspended particles in a semi-solid condition. The molecules of a gel are held together by different chemical bonds of varying strength. The stability of a gel depends upon the types of bond and the strength of the bond. During metabolic cycle of the cell, the bonds of the molecules are changed. This change of bonds is called *solution* i.e. the *sol*.

The physical properties include contractility, elasticity, cohesiveness and viscosity. Brownian movement and the streaming of cytoplasm (*i.e.* *cyclosis*) are due to viscosity of the cytoplasm.

1.3 Chemistry of Cytoplasm : "The relative amount of various protoplasmic constituents vary from cell to cell and from tissue to tissue with the age of the cell and the kind and degree of differentiation" (Wilson and Morrison, 1967). But the crude analysis of protoplasm gives us some idea regarding the kinds of substances and their relative percentages generally characteristic of living matter; those substances with percentages, kinds and location in cell are shown in the following table :

TABLE—1

<i>Substance</i>	<i>Percentage</i>	<i>Kinds</i>	<i>Location in cell</i>
Water	85 - 90	Free and bound	Nuclear sap, vacuoles, hyaloplasm
Protein	7 - 10	Albumines, globulins, histones, protamines and nucleoproteins	Membrances, hyaloplasm, cozymes
Fatty substances	1 - 2	Lipids	Membrances, hyaloplasm, inclusions
Other organic substances	1 - 1.5	Carbohydrates	Vacuoles, hyaloplasm, cell wall and storage products
Inorganic substances	1 - 1.5	Na, K, Ca, Mg, Cl, SO ₄ , PO ₄	Vacuoles, hyaloplasm, co-factors

¹ Outside the nucleus and within the cell wall lies the cytoplasm which is heterogeneous. After removing the organelles the mass of cytoplasm is called **hyaloplasm**.

Water is an absolutely essential component of the protoplasm and plays an important role in the metabolic activities of the cell. Without water, the cell can not function or even exist. It may exist as "free" i.e. as water of solution, or "bound", usually to ionised groups of proteins. Water is the medium in which all other materials are contained. In general, protoplasm may be considered to be mainly proteinaceous, and many of its properties are similar to those of colloidal dispersions of complex proteins. Besides simple proteins (e.g. globulins and histones), some complex proteins called conjugated proteins are also found. Complex protein is that protein which consists of protein and another substance, e.g. nucleoproteins of the nucleus and cytoplasmic membranes, the lipoproteins of the cytoplasmic membranes, the chromoproteins, such as hemoglobin and many enzymes.

Sugars and starches are the soluble and insoluble carbohydrates respectively. Celluloses are the component of the cell wall. The lipids are present in the cytoplasmic membranes and in the hyaloplasm. In various cytoplasmic organelles phospholipid is present which is an important lipid compound. In the cell, a variety of inorganic materials are present such as sodium, potassium, calcium, magnesium, phosphates etc.

NUCLEUS

It is the most significant component of the cell which controls various metabolic activities of the cell and contains all genetic materials. It was first discovered by Robert Brown (1835) and it has received very much more attention since its discovery than has any part of

the cell. Majority of these investigations have been concerned with the morphology, particularly of the chromosomes, but the use of new cytological techniques have contributed greatly to our knowledge of the biochemistry and physiology of the fine structure of the cell.

Nucleus is present universally in all eukaryotic cells of the plants and animals. The prokaryotic cells like bacteria have no true nucleus.

1.4 Morphology of Nucleus : The most significant component of the cell is the nucleus. Nucleus is usually centrally placed within the cell, although the position of the nucleus varies according to the cell type. Whatever its location within the cell, the nucleus is surrounded on all sides by cytoplasm.

Most plant and animal cells contain single nucleus, such cell are known as *mono nucleate cells*. The cells which contain two nuclei are known as *binucleate cell*. Such cell occur in certain protozoans like *Paramecium*, cells of cartilage and liver. There are many cells which contain many nuclei, such cells are termed as *polynucleate cells*. The polynucleate cells of the animals are known as *syncytial cells* while those of plants are known as *coenocytes*. Certain algae and fungi are the best examples of coenocyte cells.

The shape of the nucleus also varies with the cell type. The nucleus is usually spherical in shape, although ellipsoid and flattened nuclei are also not uncommon. Although the shape of the nucleus is constant, they may vary in size at different times during the cycles of cellular activity. Changes in size do not change the chromatin materials, which however, remain constant for a particular species. The individual component of the nucleus is described below :

(i) *Nuclear membrane*—Thin layer demarcating the nucleus from the cytoplasm. The membrane appears as a double-membrane structure under the electron microscope. The nuclear membrane is broken at regular intervals by pores or openings.

The electron microscopic studies of the nuclear envelope show that it consists of an outer and inner membrane. Each membrane is about 75-90Å thick and lipoprotein in nature. These membranes are separated by a space of 100-150Å (Robertis, 1970), 100-300Å (Cohn, 1970) or 400-700Å (Burke, 1970). These inter-membranous space is known as *perinuclear space*. The outer nuclear membrane sometimes is very rough due to attached ribosomes with it. Inner membrane however contains no ribosomes and sometimes associated with the chromatin.

(ii) *Cytoplasmic extrusion*—These are present between the cytoplasm and the nucleus in the pores. They usually connect the nuclear membrane and endoplasmic reticulum of the cytoplasm.

(iii) *Chromatin*—Within the limiting boundary of the nucleus there contains many thread-like, coiled and much elongated structure. These thread-like structures are known as *chromatin* or *nuclear reticulum*. They readily take basic stains. Such chromatin are visible only in the interphase nucleus. During cell divisions chromatin fibres become thick ribbon-like structure, known as *chromosomes*.

During interphase, the chromosomes are usually long and exhibit little coiling or spiraling. They resemble very fine threads so entangled among themselves. The chromosomes stain readily with basic fuchsin.

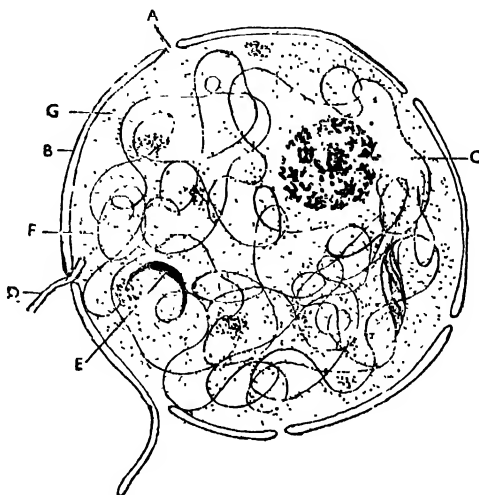


Fig. 1.2 Diagram showing the structure of the nucleus

A. Pore, B. Nuclear membrane, C. Nucleolus, D. Cytoplasmic extrusion, E. Heterochromatin, F. Euchromatin, G. Karyolymph

Certain areas of the chromatin mass stain darker than other during interphase. These chromosomal regions that stain darker than others during interphase and lighter during the cell division are known as heterochromatic regions or heterochromatin.

The differential staining reaction is due, in part at least, to the degree of coiling in the strands of the chromosomes. Where the strands are coiled tightly, there is a greater density of chromatin material and therefore a darker stain, often the denser regions appear as small, bead like bodies among the chromosomes and heavily stained regions rich in DNA. These are designated as chromomeres and they vary greatly in size.

Some evidences indicate that the heterochromatic regions have a higher RNA content than the non-heterochromatic *i.e.* euchromatic regions.

The chromomeres adhere side by side and the perfect alignment with the homologous chromomeres forms dark bands.

According to some cytologists, the chromomeres are the places where the chromonema is coiled tightly in a spring-like manner. The interconnecting materials connecting the chromomeres are placed where the chromosome is uncoiled and straight.

(iv) *Karyolymph*—It is a granular and homogeneous material. Karyolymph is also termed as matrix (nuclear sap) in which the

chromosomes lie. It is a fluid substance which escapes if the nucleus is punctured. Karyolymph fills the space between the nucleolus and the chromosomes. It is composed primarily of protein materials.

Some evidences support that the karyolymph contributes to the formation of the spindle apparatus during cell division in plants, but more recent studies show that the spindle materials is derived mainly from cytoplasmic substances.

(v) *The nucleolus*—The nucleolus is relatively a large, spherical body situated in the nucleus. The number of nucleoli present in each nucleus depends upon the species. In many plant and animal cells the nucleus may contain a single nucleolus or two or more nucleoli. In man, for example, there are two pairs of nucleoli in each diploid nucleus.

In certain cells the heterochromatic portions of specific chromosomes are always found in contact with the nucleolus. These are **nucleolar organizing regions** of the chromosomes.

During the mitotic cycle the nucleolus disappears, again one or more nucleoli reappears at the end of cell division in each daughter nucleus. There are two main components of the nucleolus, one is **pars amorpha**, which disappears and reappears at the end of cell division. The second part is **nucleolonema**, which persists throughout the cell division.

The nucleolus may play a very significant role in mitosis. Their function also appears to be related primarily to protein synthesis.

Cell division : Mitosis and Meiosis

Cell division is one of the most complex phenomena and characteristic of both sexually and asexually reproducing organisms. By this division the cellular material is divided equally between the daughter cells. This type of cell division is exhibited in all organisms, even in such primitive cell types like bacteria, although the details of the process are still uncertain. With few such exception, the mechanisms of cell division and replication is more or less similar in all plants and animals. This type of multiplication of cells usually referred to as *mitosis* where the cell divides into two daughter cells of equal size, each of which has the same number of chromosome as the parent cell. This type of division is mainly associated with the *somatic* tissues and forms the main mechanism of asexual reproduction, or vegetative reproduction. Apart from reproduction, mitosis is important in the revitalization of tissues in the adult organism particularly in the replacement of old and dying cells.

2.1 Mitosis : *Mitosis* is a process of cell division “which gives rise to new cells in the growing regions of an organism and maintains continuity of chromosome number and type.” In this process the chromosomes become *duplicated longitudinally* into two more or less equivalent parts which separate to opposite poles of the cell.

Although cell division varies widely from one species to another, but the essential features and consequence of this division are basically same in all organisms. Although the drama of the mitotic cycle centers largely in the nucleus, but the role of the cytoplasm must be taken into account in the process. We must therefore have to consider the process in its entirety. As a result of this cycle, there is a qualitative and quantitative distribution of the essential particles of heredity—the genes, which are obviously carried in the chromosomes. The behaviour of the chromosomes is therefore the most important feature of this cycle. This cycle starts at the end of the *interphase* and ends at the beginning of the next interphase. For our convenience the whole process of mitosis can be sub-divided into several stages. The stages are *prophase*, *metaphase*, *anaphase* and *telophase*. Although interphase is not listed as a stage of mitosis it is the most critical period as regards the preparation for division of the cell. In the interphase the most important feature is the duplication of DNA. Although the interphase period varies from organism to organism, but that it takes place prior to prophase is certain.

The whole process of cell division can be divided into **karyokinesis** or nuclear division and **cytokinesis** or cytoplasmic division. Although mitosis includes both the events of cell division, but in strict sense the meaning includes only the division of the nucleus.

INTERPHASE :—Since the process is involved in cell division, we must have an idea regarding the concept of interphase. It occupies the longest period in the cell-cycle. At this stage, which is often referred to as *resting stage*, the cell appears to contain the nucleus which shows a distinct nucleolus and fine thread like pro-chromosomes. The chromosomes show minimum degree of condensation or coiling. The slight coiling that exists at this stage is known as *relic coils*. The nucleolus and the cell as a whole show a maximum size.

One of the most important events of interphase is the duplication of DNA and consequently of chromosomes. This is an important step in the preparation of the cell for mitosis.

Since the chromosomes are extremely thin at this stage, they give a faint stain in the fixed condition.

PROPHASE :—It is one of the longest stage in the mitotic cycle. The cell at this stage is more or less spherical and more viscous. The chromosomes in the prophase stage appear as longitudinally coiled filaments within the nuclear envelope. The chromosomes become more stainable as prophase proceeds. This increasing visibility of chromosomes is due to increase in the state of condensation.

Each prophase chromosome is longitudinally double, which is due to two coiled filaments called **chromatids**. The chromatids are closely appressed along the entire length of the chromosome and at the same time are twisted around each other like a woolen yarn. Since the two chromatids are coiled around each other relationally, they are called *relational coiling*.

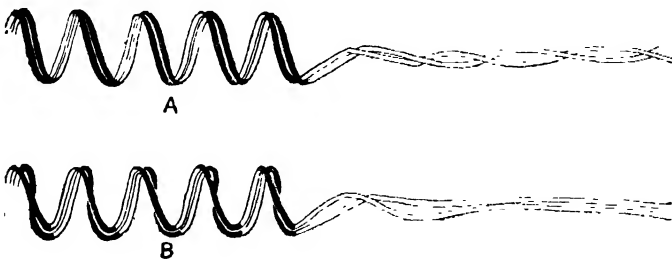


Fig. 2.1 Relational coiling of two chromatids
A. Plectonemic coiling, B. Paranemic coiling

In mitosis these chromatids cannot be easily separated and these association of coils are known as **plectonemic coiling** (Fig. 2.1A).

In meiosis, however, these chromatids can be easily separated and so these type of coiling is known as **paranemic coiling** (Fig. 2.1B).

In the early prophase the chromosomes are evenly distributed in the nuclear cavity and they do not as a rule, come in contact with

each other. They usually separate from each other due to repulsion between chromosomes. As the prophase progresses the chromosome migrates to the nuclear membrane which, however, remains till the dissolution of the nuclear membrane.

METAPHASE :—After the disintegration of the nuclear membrane the chromosomes moves towards the central region of the cell and lie

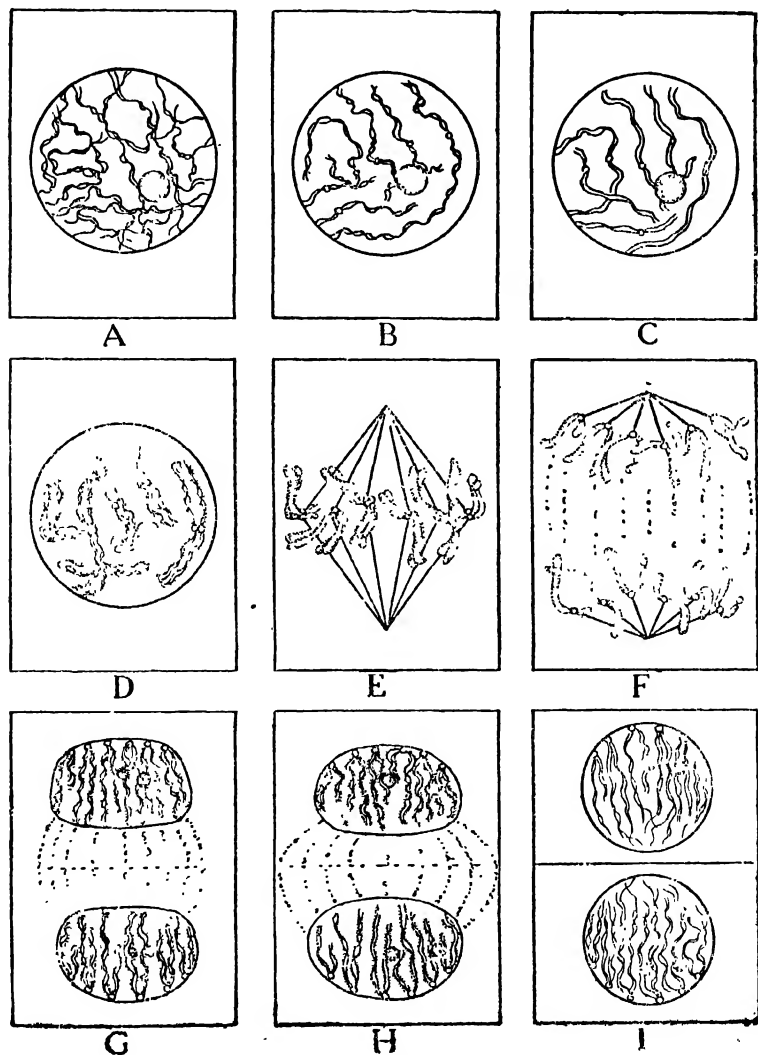


Fig. 2.2 Different stages in mitosis

A. Metaphase nucleus, B-D. Prophase, E. Metaphase, F. Anaphase, G-H. Telophase, I. Cytokinesis

freely in the cytoplasm. This stage has been termed as *prometaphase*. This movement of the chromosome ultimately making their way towards the equator is of utmost significance as it begins the metaphase proper. At this stage the chromosomes lie in the equator and arrange themselves radially in relation to the origin of the spindle. Thus the arrangement of the chromosome in the equatorial plate is that the centromere lie in the longitudinal axis of the spindle while the chromatid arms project on either side. In majority of the higher plants the spindle fibers originate as *anastral* type or cytoplasmic in origin, (i.e., fibers originates not from centroles and asters as it is characteristic of majority of animals). Some of these fibers of the spindle then attach to the centromere of the chromosomes, whereas some fibers run without interruption from one pole to the other. The former is termed as *chromosomal fibers*, whereas the latter one is termed as *continuous fibers*.

The metaphase chromosome consists of two tightly coiled chromatids and they therefore appear as the shortest and the thickest. Metaphase chromosomes are therefore the true mitotic chromosomes. At metaphase the centromere is still undivided or if divided the two halves are surrounded by a common envelope.

At the end of metaphase the force of attraction of the chromatids loses due to division of the centromere. This division gradually spreads to the chromatids, thus ultimately dividing the chromosomes. These daughter centromeres then repel, thus the chromatids separate and the migration towards the poles is ensured.

ANAPHASE :—This is the shortest of all stages in the mitotic cycle. In this stage chromatids begin to move from the equator towards the poles. The movement of the chromosomes first starts with the separation of the centromeres, while the arms of the chromatids are passively dragged along. At this stage the chromosomes become quite distinct and assumes 'V' or 'L' shaped appearance.

The movement of the chromatids in this stage possibly occurs due to some force given by the fibers by the contraction of the protein molecules of the chromosomal fibers. The movement of the chromatids may also be due to repulsion between the parts of the divided centromere. These two movements eventually help the chromatids to move to the respective poles.

As a result of this stage the chromosomes are separated into two equal numbers and so they have got the same genetic constitution. Thus the distribution of chromosomes both quantitatively and qualitatively are equal. The coiling of the chromosome may continue even during anaphase, so that the chromosomes become even more condensed than at metaphase.

TELOPHASE :—The end of the polar migration of the two groups of chromatids marks the beginning of telophase. Thus in this stage all the daughter chromosomes arrive at their respective poles. The telophase chromosomes are indistinguishable as they are very much

uncoiled at this stage. This stage like prophase, lasts for a considerable period. It starts with the uncoiling of the chromosomes, followed by the appearance of nucleolus. The formation of the nucleolus is also related with the metabolic activities of the cell. Anyway during the telophase the nucleoli appear at the nucleolar organizers or satellite zones of the chromosomes.

Thus after nucleolus, a nuclear membrane forms around the daughter chromosomes. This membrane originates from the endoplasmic reticulum that has passed on to the polar regions.

CYTOKINESIS : The division of the chromosome is followed by the division of the protoplast by the formation of a wall between the two daughter nuclei into two cells. This is known as **cytokinesis**. A cell division is not complete without cytokinesis. The process of cytoplasmic division differs considerably in plants and animals cells.

In some coenocytic algae and fungi, cytokinesis does not occur after nuclear division, as a result multinucleate thallus is formed.

In plant tissues cytokinesis is accomplished by the formation of a *cell plate*. The cell plate formation depends upon the presence of elements of the reticulum which gathers in the equatorial region of the cell between the daughter chromosomes and forms the **phragmoplast**. The fibrils of the spindle fibers widen and touch the side walls. Thereby a barrel shaped structure is formed and which finally disappears. Next protoplasmic materials are deposited in the form of granules or droplets in the equatorial plane of the spindle. They finally adhere to each other forming a plate called **cell-plate**. It is transformed into a middle lamella by physical and chemical changes and afterwards new cellulose materials are deposited over the middle lamella.

Thus the two important phases of cell division are the division of the nucleus known as **karyokinesis** and the division of the cytoplasm known as **cytokinesis**. In most plants and animals, the basic mechanism of division is the same, although it differs in the formation of the spindle, mode of cytokinesis and the coiling cycle of the chromosome.

2.2 Meiosis : Since the chromosome number of the cells of the individual belonging to the same species is constant, so in sexually reproducing organisms there must be a compensatory mechanism which reduces the chromosome number during the life cycle of an individual. The constancy of chromosome number is repeated generation after generation. In sexually reproducing organism the doubling of the chromosome number, due to union of two gametes, is compensated by the halving of the zygotic number sometime during the life cycle of an individual. The reduction in number of chromosome is accomplished by a special type of cell division called **meiosis**. Meiosis, therefore, may be defined as a special series of divisions by means of which the transition from sporophytic to gametophytic tissue in plants and the formation of gametes in animals is normally accomplished. In this type, the chromosome number is *reduced* to

half and partner or homologous chromosomes are segregated. This consists of two successive nuclear divisions, the *first* and *second meiotic division*, during which chromosomes divide only once.

The process although a complicated one, yet in its essential feature it is essentially same wherever it is encountered. Although the two processes are essentially same, still with reference to biochemical properties of the cell, meiosis is much less known than mitosis. The first important puzzle of the meiotic cycles is the question regarding initiation or induction of meiosis. There must occur certain physiological changes for the transition of a particular cell from mitotic behaviour to meiotic one. One important possibility of such a behaviour is the production of certain meiosis-initiating substances from the adjacent somatic tissues. The nature of these substances may be hormone or hormone-like. The non-sporogenous tissues surrounding the spore mother cells, secrete these hormone-like meiotic initiating substances which then divide meiotically to produce spores. Another possibility is the ratio between RNA and DNA. If the ratio of RNA : DNA is high, mitotic division will occur, if however, the ratio is low, meiosis will take place. Anyway whatever may be the possible explanation of such complex problems, for our convenience the whole process of meiosis can be sub-divided into several stages like mitosis.

FIRST MEIOTIC DIVISION

The most significant feature of meiosis is that the prophase of the first meiotic division is long and the chromosome complements pair and exchange of hereditary materials takes place. Like mitosis the whole cycle of meiosis can be arbitrarily separated into following four stages of which prophase is the longest and genetically most significant.

PROPHASE I :—Meiotic prophase is characterised by a decided increase in the volume of the nucleus. This is due to an increase in hydration. Prophase-I of meiosis is extremely long and comprises several sub-stages. Like the major division of the meiotic cycle these sub-stages are somewhat artificial.

(i) *Leptotene*—With the increase of cell and nucleus *leptotene* starts. The chromosomes appear as long threads and distinct from one another. Since the chromosomes are elongated, individual chromosomes are not identifiable. At the beginning of leptotene the individual chromosomes remain uncoiled, but gradually small coils develop.

The leptotene chromosomes are arranged in the nucleus in two different ways. In some cases the chromosomes are densely aggregated to one side, leaving the remaining portion of the nucleus clear. This type of orientation is known as *synizesis*. In other cases they are *polarized*, i.e. the ends of the chromosomes are drawn towards the side of the nucleus where the centrosome is located, while the

remaining portion of the chromosomes extend towards the center of the nucleus. Polarization, however, is less frequent in higher plants as no definite centrosome is present in plants.

(ii) *Zygotene*—In zygotene, the chromosomes unite in identical pairs, each of them cohering with its homologue. These chromosomes are also known as homologous chromosomes. So pairing or **synapsis** of homologous chromosomes is the striking feature of zygotene. These paired chromosomes are known as **bivalents**. The pairing of the chromosomes takes place part by part and proceed in a zipper-like fashion along the length of each chromosome. It is important to realize that the pairing of the homologues is very intimate one which is not merely between homologous chromosomes but always between strictly homologous regions. The pairing process is of two types. In some cases the pairing begins at the ends of the chromosomes and proceeds towards the centromere region when it is called **proterminal** or the pairing may start at the centromere and proceed to the ends when it is called **procentric** or it may be random without any definite sequence.

The coiling of the chromosomes still continues during these substages and as a result the chromosomes becomes shorter and thicker.

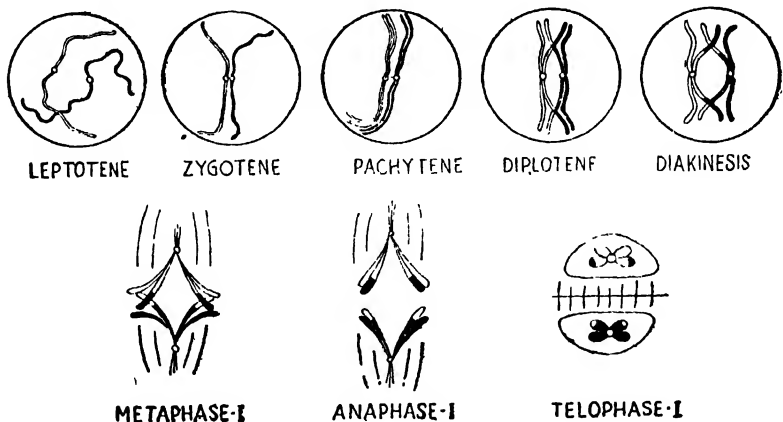


Fig. 2.3 Crossing over between homologous chromosomes showing diagrammatically during the first meiotic cell division

(iii) *Pachytene*—It starts with the complete pairing of the chromosomes. The chromosomes at this stage contract longitudinally and becomes still shorter and thicker. The chromosomes at this stage are readily identifiable and characteristic euchromatic and heterochromatic regions are visible late in the pachytene stage. Each chromosome forms two chromatids and each synapsed pair becomes visible as double so that the whole structure is four-stranded. Each thread of pachytene is, therefore, a tetrad of chromatids.

(iv) *Diplotene*—At the end of the pachytene the synaptic attraction between the homologues suddenly come to an end and the homologous chromosomes separate from each other except that they are held at certain points. The two out of four strands of each bivalent therefore form an 'X'. Each of these places or points is known as *chiasma*. When only one chiasma has formed, the bivalents appear as a cross. When two are formed, it looks like a ring-shaped appearance, if three or more chiasmata are formed, the bivalents appear as a looped configuration.

During the diplotene the shortening of bivalents or homologous chromosomes goes on; the component four chromatids are evident in each paired chromosome. At the time of separation of chromatids, exchange in partners by crossing over takes place. Chiasmata may be *terminal* (found at the ends of the chromosome) or *interstitial* (found any where along the arms of the chromosome). It was thought that from the interstitial ones terminal chiasmata originate gradually by the movement of the chiasmata towards the ends of the chromosomes in the process of terminalization.

(v) *Diakinesis*—This is the last sub-stage of prophase. The distinction between diplotene and diakinesis is not very sharp although the chromosomes become shorter still as their chromonemata continue to coil.

During this sub-stage the bivalents are distributed to the periphery of the nucleus and are well separated. It is, therefore, the most favourable stage for counting the chromosomes.

The nucleolus at this stage begins to disappear and no longer visible at the end of the prophase-I. As a result of the disappearance of the nuclear membrane at this stage, the chromosomes are released in the general mass of cytoplasm.

At the end of prophase-I the spindle fibers begin to originate to establish the poles of the cell and it will determine the axis of orientation of the chromosome in metaphase-I.

METAPHASE I:—By the complete disappearance of the nuclear membrane and appearance of spindle fibers the prophase-I ends and the metaphase-I begins. The bivalents at this stage move to the equator with their centromere towards the poles and their arms towards the equator. In mitosis the undivided centromere of each chromosome lies on the equatorial plate whereas in meiosis each bivalent has two undivided centromeres which lie on the long axis of the spindle. The two centromeres of a bivalent then repel each other. In the mean time the spindle fibers extend between the poles and are attached only to the centromere regions of the chromosomes.

ANAPHASE I:—Movement of the chromosomes towards the poles represents the anaphase. As the centromeres move first they carry with them the arms of the chromosomes, as a result of this movement complete terminalization of the chiasmata occurs. Thus the homologues are free from each other, each of which now consists of two

distinctly separated chromatids which are attached only on the centromere region.

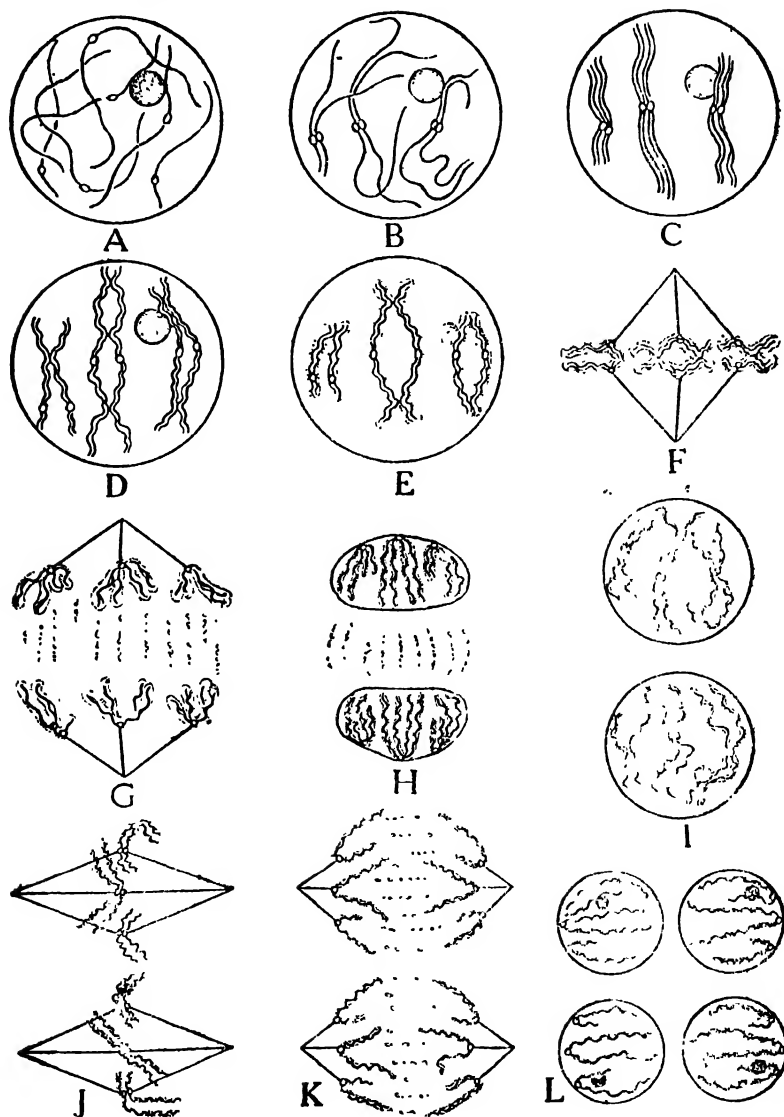


Fig. 2.4 Different stages in meiosis

A-E. Prophase-I (A. *Leptotene* B. *Zygotene* C. *Pachytene* D. *Diplotene*
E. *Diakinesis*) F. Metaphase-I. G. Anaphase-I H. Telophase-I
I. Prophase-II J. Metaphase-II K. Anaphase-II
L. Telophase-II

As a result of this movement, the chromosome number is reduced to haploid from diploid state. This is the essential difference between mitosis and meiosis.

TELOPHASE I :—In telophase-I the chromosomes elongate by loosening their coils, the nucleolus reappears and a nuclear membrane forms around each polar group of chromosomes. After the first meiotic division cytokinesis may or may not occur, as a consequence two cells or two nuclei in the common mass of cytoplasm may occur.

The two daughter cells or nuclei thus formed pass through a short stage called **interphase stage** or **interkinesis**. The cell or nuclei then passes through division II; the duration of the interphase is variable.

SECOND MEIOTIC DIVISION

This division, often known as **meiotic-mitosis**, starts immediately after the first meiotic division and is termed as **equational division**.

PROPHASE II :—Matrix appears and chromosomes are arranged in diads.

METAPHASE II :—In this stage bipolar spindle is formed again and all the chromosomes are arranged in the equatorial plane of the spindle.

ANAPHASE II :—Diads consisting of two chromatids move apart and run towards the two poles and this movement takes place along the fibers. The centromeres move in the usual manner and different shapes are assumed by the chromatids.

TELOPHASE II :—Daughter nuclei are formed from the chromatids after its reorganisation at the poles and finally four nuclei are formed. Each nucleus possesses a set of haploid chromosomes and chromatid of each of the tetrads of the prophase-I stage.

CYTOKINESIS :—Finally cytokinesis takes place forming four cells and each cell-nucleus consists of a haploid number (reduced number) of chromosomes.

Significance of Meiosis—It is necessary in the life cycle of sexually reproducing organisms. The significance of meiosis is the *reduction in number of chromosomes* in the reproductive cells e.g. spores, gametes etc. If the reduction division or meiosis would not have taken place then in the generations of succeeding sporophytes the chromosome number in their somatic (body) cells would have been $2n$, $4n$, $8n$, and so on. That is not possible as number of chromosomes in the somatic cells of an individual sporophyte is always constant and the number is constant for a particular species. In order to maintain the constant number of chromosomes of species, its reproductive cells must undergo reduction divisions or meiosis.

Since crossing over is an essential feature in the meiotic cycle, *exchange of genetic materials* is an evident feature. The haploid

cells resulting would, therefore, contain a mixture of paternal and maternal chromosomes.

As a result of this random segregation of paternal and maternal chromosomes due to breaking of chiasma, the haploid cell (*i.e.* gametes) formed will, therefore, have a *variable combination of genes*.

In sexually reproducing organisms, since these gametes contribute to next generation through fertilization, the individual formed will also exhibit a *genetic variation*. It is this variability which brings about the evolution in organisms.

2.3 Comparative account of Mitosis and Meiosis :

MITOSIS

1. Mitosis is characterised by only one nuclear division which is involved with the duplication of the chromosome.

2. Mitotic division occurs mainly in the somatic cells of the organisms. It is the chief process of reproduction in many unicellular organisms.

3. The only purpose of the mitosis is to increase the number of somatic cells in the body.

4. Synthesis of deoxyribonucleic acid (DNA) takes place in the interphase.

5. Prophase stage is short and does not divided into sub-stages.

6. Longitudinal splitting of the chromosomes occurs forming two sister chromatids. Chromosomes appear as double threads.

7. The two separated homologous chromosomes are not attracted toward each other. So no bivalents, chiasma and crossing over occurs.

MEIOSIS

1. Meiosis involves two nuclear division where the chromosomes are duplicated only once.

2. Meiosis always takes place in the reproductive cells of the sexually reproducing organisms.

3. Meiotic division is of great significance in the sexually reproducing organisms in maintaining the chromosome number constant. This is usually maintained by fusion of two haploid gametes to form diploid zygote.

4. Synthesis of DNA proceeds upto prophase I.

The interphase after the first meiotic division is not a synthetic phase.

5. Prophase stage is much long and divided into several sub-stages viz. *leptotene*, *zygotene*, *pachytene*, *diplotene* and *diakinesis*.

6. No longitudinal splitting of the chromosomes which appear as single threads.

7. During the zygotene of the prophase stage, two homologous chromosomes attract each other forming bivalents. Splitting of the chromosomes occurs forming

MITOSIS

8. Chromosomes arrange themselves in the equatorial position and the spindle fiber attach to the centromeric position of each chromosome.

9. The centromere divides into two sister chromatids which move towards opposite poles, thereby maintains the somatic number.

10. Each chromosome whether their origin is paternal or maternal is divided longitudinally, therefore, two identical daughter cells are formed at the end of mitosis.

11. At late metaphase, the initial movement of the chromosomes is due to repulsion between the parts of divided centromere.

12. At the telophase, the chromosomes uncoil as thread like structures, two diploid ($2n$) daughter nuclei are reconstituted.

13. In mitosis there is no second division.

14. At the end of mitosis two cells are formed with same number of chromosome, qualitatively they are also identical.

MEIOSIS

four strands, after that exchange of segments between two i.e. paternal and maternal chromatids takes place. The chromosomes of the pair begin to separate out after the exchange of genetic materials between the homologous chromosomes (crossing over).

8. Each bivalents arrange themselves in the equator so that the centromeres get attached with the spindle fiber.

9. The homologous chromosomes move to the opposite poles without any division of the centromere in the first metaphase.

10. The arrangement of chromosomes at the equatorial plate is in such a manner that either paternal or maternal material goes to one pole at the metaphase-I. At the end of first meiotic division the two daughter cells are not identical.

11. At late metaphase-I, the initial movement of the chromosomes is due to repulsion between the centromeres of homologous chromosomes.

12. At telophase-I, two haploid (n) daughter nuclei are reconstituted.

13. There are two cell divisions in meiosis. The first one is called reduction division and the second one is the equational division. In metaphase-II, the centromeres divide and separation of sister chromatids takes place.

14. At the end of meiosis, 4 cells are formed each with n number of chromosomes, qualitatively they are not identical.

CHAPTER 3

The Chromosomes

Of all the cytoplasmic organelles present within the cell, the *chromosomes* are the most complex and least understood as regards their molecular organization and mode of function. Their presence in the cell was first demonstrated by Hofmeister long before they were actually termed as 'chromosomes' by Waldeyer in 1888.

Since then, considerable advance has been made regarding the structure and behaviour of the chromosomes. These are nuclear components with special organization and function.

The chromosomes replicate with great regularity during the cell division and their morphologic and physiologic properties are maintained generation after generation. Thus the genetic information of the parent cell is maintained from one generation to the next through the chromosomal material. So, their importance in heredity has been amply demonstrated.

Although much has been discussed in this line, but despite the thorough attention many problems still remain unsolved. In recent years many of the cytological problems have been studied jointly by the chemists and the physicists. Although the organisms contain variable number of chromosomes in different species but they have basically the same physical and chemical organization. Here in this chapter, the organization of a typical chromosome as well as their variation will be discussed.

3.1 General Morphology of the Chromosome : The number of chromosome in a particular organism is always constant, although their number varies greatly from one species to another. The lowest number of chromosome found in round worm (*Ascaris megalocephala*) which has a haploid number of 1. In plants *Haplopappus gracilis* (Compositae) has a haploid number of 2. In many protozoa several hundred of chromosome are found to be present in diploid cells. Although the chromosome number varies considerably but the advanced plants and animals have the chromosome number within a limited range. The basic haploid number of chromosomes in an organism is called a **genome**. In diploid cell, there are two haploid sets and each chromosome of each haploid set has a partner or homologue in the other set. As the chromosomes reach their maximum contraction at metaphase and anaphase, the chromosome characteristics can be best studied during these two phases. Since the degree of coiling and the actual length of the strands vary with individuals, with cells and with organisms, the measurement of chromosomes are not exact. Anyway the average length of the chromosomes range from 0.1μ to 30μ in length and from 0.2μ to

about 2μ in diameter. The largest known chromosomes are found in *Trillium grandiflorum* whose metaphase configuration is about 32μ in length. Generally, the length of chromosomes in plants with fewer number of chromosomes are larger than plants with many chromosomes. Monocotyledones generally have larger chromosomes than the dicotyledones.

TABLE 2
Chromosome number of some plants

Plants	Chromosome number (diploid)
Rice (<i>Oryza sativa</i>)	24
Wheat (<i>Triticum aestivum</i>)	42
Barley (<i>Hordeum vulgare</i>)	14
Onion (<i>Allium cepa</i>)	16
Corn (<i>Zea mays</i>)	20
Cotton (<i>Gossypium hirsutum</i>)	52
Tomato (<i>Lycopersicon esculentum</i>)	24
Garden Pea (<i>Pisum sativum</i>)	14
Broad Bean (<i>Vicia faba</i>)	12
Potato (<i>Solanum tuberosum</i>)	48
Tobacco (<i>Nicotiana tabacum</i>)	48

The chromosomes usually appear as cylindroids in nature and they stain intensely with basic stain and Feulgen method. They can be easily observed *in vivo* by phase contrast microscope.

The morphology of the chromosome varies from cell to cell and the major changes are associated with the cell division. The electron microscope technique does not provide any good idea for detailed description of the ultra structures of the chromosome either at anaphase or any other stages. The following description of the chromosome is based on the metaphase configuration since during this stage the chromosomes are maximum coiled and can be studied properly.

Chromonemata : Each chromosome consists of two spiral structure known as chromonemata (singular chromonema). Chromonema consists of several microfibrils. According to some, 64 such microfibrils comprise a single chromonema. These are said to be gene-bearing portion of the chromosomes, although some non-genic portion is also associated with it.

Regarding the number of chromonema in each chromosome, several possibilities have been suggested. Majority of the scientists are of opinion that each chromosome contains two such spiral chromonemata. Others are of opinion that there are four chromonemata in each chromosome (Trosko and Wolff, 1964).

Majority of the evidence favour the view that interphase chromosome consists of certain coiled or folded appearance to produce

prominent beads or **chromomeres**. The term was first proposed by Balbiani in 1876. The morphologic interpretation of the chromomeres has varied widely. According to Pontecorvo (1944) chromomeres are said to be structurally different from the remaining chromonema and represent condensation of nucleo-protein materials. This view has been later on supported by Kaufmann (1948). Ris (1945), however, suggested that chromomeres are formed due to differential coiling of a single fiber of a chromosome. The latter view has been supported by a large number of workers through electron microscope observation.

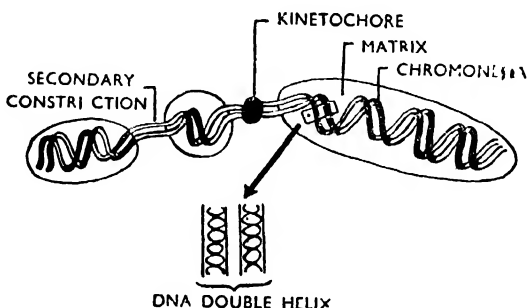


Fig. 3.1 A typical somatic chromosome in mitosis. Satellite is shown at the extreme left hand side

The chromomeric structure of salivary gland chromosome and lampbrush chromosome are not comparable to those of ordinary meiotic chromosomes.

Regarding the function of the chromomere no definite conclusion has been made.

Matrix: The chromonemata are embedded in a mass of achromatic materials known as **matrix**, the outer boundary of which is limited by a sheath or **pellicle**. Both the matrix and the sheath are the non-genic part of the chromosome.

The term matrix has been employed by different cytochemists in different meaning. Although the reality of the matrix has been challenged by a number of workers including Darlington (1937) and Ris (1945), but there are many reasons for believing that it does actually exist (McClintock, 1934; Iwata, 1940; Swanson, 1943; Kaufmann, 1941).

Regarding the structure and function of the matrix it is still a debatable question. Most probably it helps to keep the chromonemata within bounds, but its function regarding the contraction of chromonemata as suggested by Kuwada (1939) is not certain. They presumably function as an insulating sheath for the genes.

Centromere—Within the chromosome, a constriction is located at a point where the arms of a chromosome meet. This region is

specially connected with the attachment of the spindle and is therefore related with the movement of the chromosome. This constricted region is termed as centromere by Darlington or kinetochore by Schrader or kinomere by Huskins.

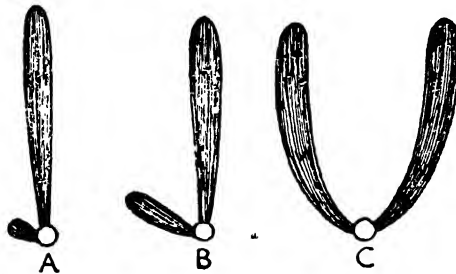


Fig. 3.2 Three morphologic types of chromosomes
A. Acrocentric, B. Sub-metacentric, C. Metacentric

Centromeres commonly appear as relatively achromatic in nature and are indispensable. Since a centromere delimits the arms of the chromosome it is also termed as **primary constriction** or **centric constriction**.

Centromere may occupy any position along the chromosome. The portion of the chromosome on either side of the centromere is known as **arm**. It may be equal or unequal depending on the position of the centromere. If the centromere is at or near the mid-point, the chromosome is described as **metacentric**. If it is at the end, the chromosome is described as **acrocentric** or **telocentric**. If it is in any other position, the chromosome is described variously as sub-metacentric or sub-acrocentric (Fig. 3.2).

Usually one centromere is present in each chromosome (**monocentric**); the evidence for the existence of two (**dicentric**) or more (**polycentric**) centromere in a chromosome is also not uncommon. **Dicentric** chromosome is the characteristic feature of some species of wheat, where as *Luzula purpurea* (Juncaceae) is of polycentric type. In hemipterous insects the centromeres are not localized but are located along the entire length of the chromosome. This is termed as **diffuse centromere** (Schrader, 1935; Ris, 1942). Diffuse centromere represents a primitive type from which the localised type arose.

Regarding the structure of the centromere various interpretations have been made. In its basic structure most of the centromeres appear as one or more chromomeres with interchromomeral fibrillae. These fibrillae are nothing but the chromonemata. The number of the fibrillae are, however, many in a centromere. The fibrils of the centromere remain uncoiled or less coiled than those of the rest of the chromosome. It is for this less coiled structure, the centromere stain lightly than the rest of the chromosome. The structure of the centromere has been described by Schrader (1953)

and Lima-de-Faria (1959). It may be represented as a modified chromonema or as a central granule or spherule connecting the chromonemata or with a number of micelles or with oriented micelles so as to facilitate misdivision in transverse way. The structure of centromere is represented in Fig. 3.3 and 3.4.

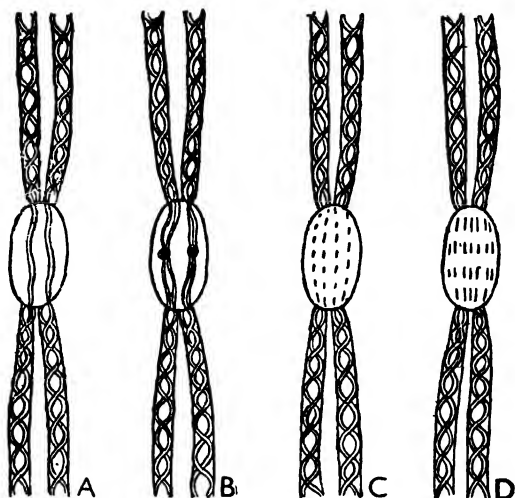


Fig. 3.3 Hypothetical structure of centromere as proposed by Schrader (1953)

A. Regionally modified portion of the chromonemata, B A granule or spherule connecting the chromonemata, C. With a number of micelles, D. With oriented micelles

The centromere is considered as an autonomous organelle whose function is yet uncertain. Darlington considered it a gene or chromomere. The role of centromere in the movement of chromosome is definite and in addition it appears to be at least partially responsible for the formation of chromosomal fibres in the spindle so they are said to be organizer of the achromatic spindle.

SECONDARY CONSTRICTIONS :—In addition to primary constriction, certain chromosome of the cell contains an additional constriction in its body which is visible by the light microscope and is termed as **secondary constriction** and the part of chromosome as **satellite bodies**. This region is also termed as *nucleolar organizing region* since it is connected with the recognition of the nucleolus at the end of cell division. If the secondary constriction is near the end of the chromosome, a small portion of chromosome lies beyond it. This is satellite chromosome which is a round, elongated body separated from the rest of the chromosome by a small light staining strands. This part of the chromosome is also termed as **sat-chromosome**, the length of which varies from the length of a chromosome to a perceptible dot. In some cases terminal and sub-terminal secondary

constrictions are present and form the characteristic feature of a particular genome.

EUCHROMATIN AND HETEROCHROMATIN :—From the view point of cytologists and cytogenetisists, the chromosome contains two kinds of chromation—euchromatin and heterochromatin. From the genetic point of view euchromatin is considered to be that part of the chromosome which carries the genetic materials whereas heterochromatin part of the chromosome is relatively inert. Mostly this

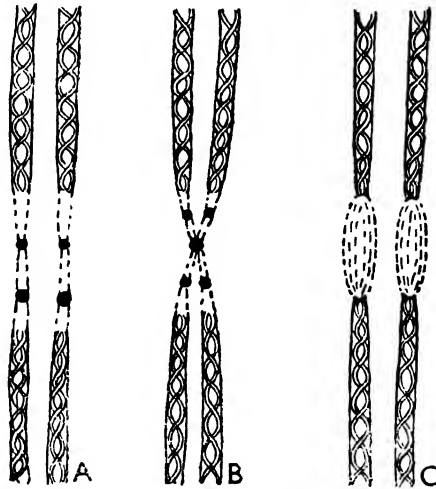


Fig. 3.4 Structure of centromere as proposed by Lima-de-Faria (1959)

segment of the chromosome can be deleted without producing any phenotypic change. Regions near or adjacent to the centromere are heterochromatic in nature.

In many species, some of the sex chromosomes may be heterochromatic in nature and so they are almost genetically inert. In *Drosera* chromosome only the tips, whereas in *Vicia faba*, *Drosophila* and in many others it is the centric regions which are heterochromatic in nature.

3.2 Special Chromosomes

(1) 'Salivary gland' type Chromosome : These are one of the giant chromosomes of larval stages of certain Diptera which are characteristically different from more typical sometic cells of the same organism. Although such chromosomes were reported first in 1881 by Balbiani but were not studied extensively until 1930. They are found only in certain tissues including the salivary glands, the Malpighian tubules, and some regions of the gut and trachea. The organisms in which they occur include *Drosophila*, *Sciara*,

Rhynchosciara and *Chironomus*. The salivary type chromosome are often of enormous size, sometimes about 100 times more than those of the corresponding somatic chromosomes at metaphase. Because of the presence of the numerous chromonemata this giant chromosome has been named polytene chromosome.

According to Alfert (1954) these chromosomes can be seen to be composed of two homologous chromosomes which are closely paired and loosely twisted around each other. Since they are really paired units they are present in the diploid number in the tissue in which they are found. The normal chromosomal staining characteristic shows distinct alternating chromatic and achromatic regions of variable width and which are referred to as the "bands" and "interbands" respectively. The bands are composed of chromomeres of individual chromonemata in a linear array perpendicular to the axis of the chromosome. Thus the bands are due to tighter coiling of the chromonemata in certain regions than in others (Fig. 3.5). Regarding the chemical difference between bands and interbands is that the bands are rich in DNA and contain RNA and basic protein are well. The interband regions, however, contain less nucleic acid together with

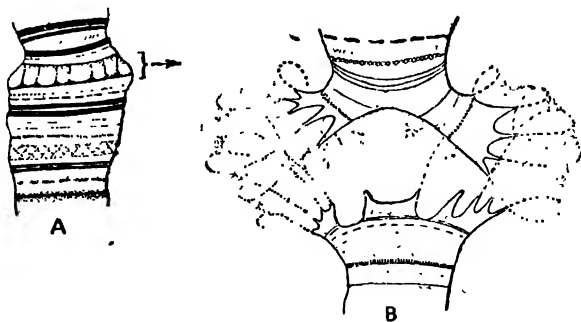


Fig. 3.5 A portion of salivary gland chromosome (A) and its appearance after formation of a Balbiani ring (B)

basic protein. Although it cannot be implied, that a band represents a gene, but some genetic loci can be associated with specific bands. In *Drosophila*, the studies on cytological and genetic maps clearly identify the sites of genetic activity from the bands. Radiation studies have substantiated these findings. The interbands have not been studied intensively as the bands but changes in the chromosomes during larval development suggest that they too are genetically active.

During the development of larvae of certain dipterans, some of the band and interband regions of the chromosomes exhibit swelling or "puffs". The formation of puffs generally occurs at single bands or interbands, but it is not confined only to a single band in the chromosome since adjacent loci may form puffs simultaneously with or independent of other loci. Some regions display larger puffs than

others. These large puffing regions are called **Balbiani rings**. Beermann (1956) suggested that the chromonemata running through the specific band of the salivary gland chromosome extend laterally to form a series of small loops which seem to stretch the chromosome to a wide diameter. These loops form the Balbiani rings and give the chromosome a fuzzy appearance.

The puffs are the result of interaction of specific locus of the chromosome and the nuclear environment. The production of chromosomal materials increases the diameter of the chromosome at a specific point and tends to spread adjacent bands apart. According to Beermann (1956) and Pavan (1958) the formation of puffs or Balbiani rings is intimately connected with the differential gene activity.

(2) **Lampbrush Chromosome** : These are the largest known chromosomes found in the oocytes of many vertebrates. They are enormously enlarged and can be seen with a naked eye. In the meiotic prophase they appear to be brush-like in their appearance. Although it has been first described by Flemming in 1882, the name "lampbrush" have been given by Ruckert in 1892.

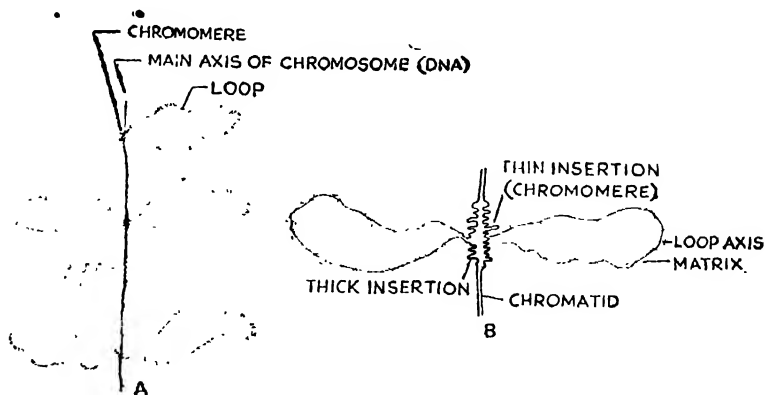


Fig. 3.6 A. Lampbrush chromosome structure with paired lateral loops,
B. Enlarged portion of a loop showing chromomere with attached lateral loops

These chromosomes contain a central chromosomal axis from which project a series of lateral loops (Fig. 3.6). Though the axis have been found to be optically single, but there are strong evidences to suggest that it is double in nature. The loops actually project out from the dense region of the chromosome which is comparable with the chromomeres of the normal chromosomes. The centromeric region bears no lateral projections. It is evident from the work of Gall (1956, 58) central axis i.e. the loops are an integral part of the chromonemata. The brush-like characteristic of the chromosome reaches its maximum development in the diplotene of the first meiotic

division, it however attain its normal configuration towards the first metaphase.

The main axis of the chromosome contain DNA and protein and since it is continuous with the loop axis, the loop axis is also found to be formed with DNA and protein. The matrix of the loop, however, composed of RNA and protein. The function of the lampbrush chromosome may therefore involve the synthesis of RNA and protein. This type of chromosomal activity is comparable to the asynchronous synthesis of DNA in the nuclei of many other organisms. The loops are, therefore, correspond to genetic loci which are synthetically active only when loops are present.

Although lampbrush chromosomes have been observed in fish, birds and salamander, the oocyte nuclei of newt (*Triturus viridescens*) contain the longest chromosome, nearly 3 times longer than the longest dipteran salivary gland chromosome. The morphological variation exhibited in the structure of the loops clearly suggest that each loop or loop pair represents a different genetic locus responsible for the formation of particular cell products (Gall, 1958).

(3) **Accessory or Supernumerary Chromosomes or B-chromosome** : It is another special type of chromosome, first observed by Wilson (1905) in a hemipteran insect. Subsequently their occurrence in higher plants have been pointed out by Darlington (1937), Hakansson (1945), Fernandes (1946), Melander (1950) and many others. These special chromosomes have been variously termed as accessory chromosome, supernumerary chromosome or B-chromosome.

These chromosomes are much smaller than the normal chromosome. Their number also varies depending on organisms. The presence of these chromosomes in higher plants have got no detectable phenotypic expression. They are practically genetically inert. The staining characteristic clearly indicate that they are heterochromatic in nature. The greatest variation have been observed in *Tradescantia* where the supernumeraries are euchromatic in nature ; while those of maize (*Zea mays*) they are partly heterochromatic and partly euchromatic.

There is a great doubt regarding the origin and ancestry of these chromosomes. Regarding the origin of supernumerary chromosome in plants there is still a great doubt. In *Metapodium terminalis* (hemipteran insect) they have been found to have originated by the deletion of the Y-chromosome. In *Metapodium* the chromosome contain diffuse centromere, so there is every possibility of preserving the chromosome fragments.

Of all types the B-chromosome of maize have been extensively studied. According to Longley (1938) they are specially distributed in many of the strains of Indian maize. In some cases their occurrence in large number may cause a reduction in vigor and fertility. So according to same they are not definitely genetically inert as had been previously supposed. The detailed morphology of the B-chromosome of maize have been put forwarded by

McClintock (1933). According to him no portion of the B-chromosome is homologous with any region of the other chromosomes.

Besides their segregation in the microspores of plants, they may segregate irregularly at meiosis, undergo somatic non-disjunction and can frequently change in the morphology of the chromosome through fragmentation. Muntzing (1945-46, '50) clearly described the different forms of the B-chromosome in *Secale* and Melander (1950) in the fresh water turbellaria (*Polycelis tenuis*).

3.3. Chemical Nature of the Chromosome : The major chemical constituents of the chromosome are nucleic acids, histone and non-histone proteins. In addition to these constituents, calcium is also found to be associated with nucleic acid (Barton, 1951 ; Mazia, 1954), although its actual correlation with the nucleic acid is problematical. According to Mazia, calcium is important in binding the chromosomes together.

The association of nucleic acid, protein and calcium to form a nucleoprotein complex is a problematic question. Each of the several nucleic acids and proteins in the chromosome fiber has a vital position and an equally vital function.

1. NUCLEIC ACID :—Nucleic acids have the most complex chemical structure and are of utmost biological importance. They

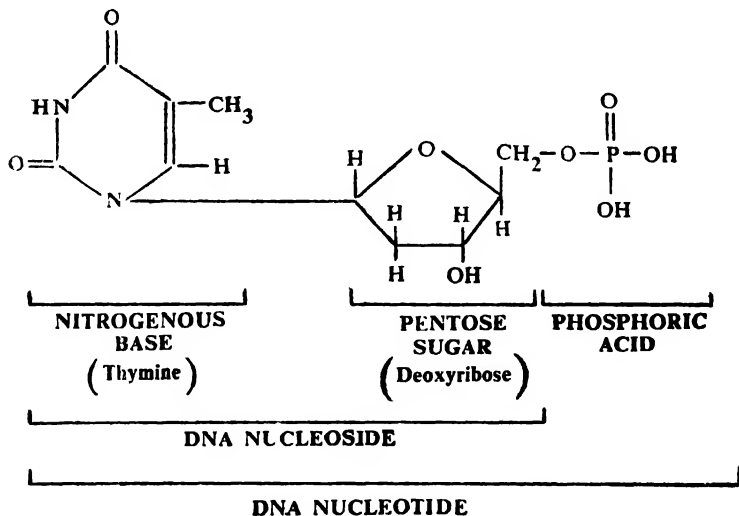


Fig. 3.7 Structural relation between a nucleoside and a nucleotide

are usually formed from a sugar moiety (ribose or deoxyribose), nitrogenous bases (purines and pyrimidines) and phosphoric acid. The combination of the single phosphoric acid, pentose and a purine or pyrimidine is termed as nucleotide. The combination of pentose (sugar) with the base (purine or pyrimidine) constitutes a nucleoside.

Nucleic acid is, therefore, a polynucleotide containing many units of nucleotides. All living organisms contain nucleic acids which are of two biological types *deoxyribonucleic acid* (abbreviated as DNA) and *ribonucleic acid* (abbreviated as RNA). Bacteria and higher plants contain both DNA and RNA. Some viruses (e.g. tobacco mosaic virus and poliomyelitis virus), however, contain only RNA whereas bacteriophages and vaccinia contain only DNA.

A. *Nitrogenous bases* (i) *Pyrimidine*—Pyrimidine bases are mainly derived from pyrimidine. *Cytosine*, *thymine* and *uracil* are the important pyrimidine bases. Cytosine is present both in DNA and RNA, thymine is present only in DNA and uracil only in RNA. In some cases 5-methyl cytosine and 5-hydroxymethyl cytosine are also present.

(ii) *Purine*—Purine comprises mainly *adenine* and *guanine* which are present both in DNA and RNA. There is a specific relationship between the purine and pyrimidine bases in DNA as a particular purine always pairs with a particular pyrimidine. The ratio of adenine (A) and thymine (T) is 1 : 1 and that of cytosine (C) to guanine (G) is 1 : 1. It has also been found that in some DNA AT predominates while in others CG predominates. Thus the ratio of base pair $\frac{A+T}{C+G}$ is not always 1 : 1 but ranges from 0.42 : 1 to 1.85 : 1 depending upon organisms.

B. *Pentoses*—There are two types of pentose sugars : *ribose* and *deoxyribose*. In case of deoxyribose one oxygen atom of the second carbon position is lacking. Ribose sugar is present in RNA whereas deoxyribose is present in DNA. Deoxyribose is responsible for Feulgen reaction and so specific for DNA.

C. *Phosphoric acid*—Phosphoric acid actually connects the two pentose sugars of two consecutive nucleosides. The union is between third and fifth carbon position of the sugars.

THE WATSON-CRICK MODEL OF DNA :—Watson and Crick (1953) proposed a helical model for DNA based mainly of four nucleotides, each of which has a different nitrogenous bases. Further work on X-ray diffraction was made by Wilkins and Franklin and after their discovery, the DNA molecules were found to compose of two long polynucleotide chain, that run in opposite directions forming a double helix, around a central axis.

The Watson-Crick model for DNA is specially important as it explains better the physico-chemical and biological properties of DNA and specially its duplication within the cell. The relatively stable, long strands forming the spiral as proposed by Watson-Crick are made up of sugar and phosphates (Fig. 3.9). They are connected crosswise with the nitrogen bases by hydrogen bonds. These two firmly connected chains are coiled around an axis and form a double helix. In each cross link the bases are arranged in such a way that a parti-

cular purine connects with a particular pyrimidine. Since the chemical analysis showed that 1 : 1 relation existed between adenine (a purine) and thymine (a pyrimidine) and between guanine (a purine) and cytosine (a pyrimidine) the connection is between adenine-thymine and cytosine-guanine. The pairing of the organic bases may be arranged in the following way :

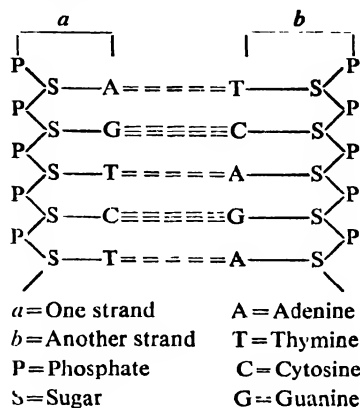


Fig. 3.8 Section of helix of DNA

The direction of one helix is opposite to the other. The dimensions of the double helix is about 20\AA units and one full turn of the helix traverses a distance of about 34\AA and it approximately contains 10 nucleotide pairs.

The aligned nitrogenous bases are **complementary**, adenine always paired with thymine and guanine with cytosine (refer Fig. 3.8). By virtue of this base sequence in its helical structure, the DNA molecule carries genetic information among the organisms. Since the two components of DNA (sugar and phosphate) are constant the information is coded by the sequence of the four bases. Thus the code has only a four-letter alphabet. The letters of the code are A-G-T-C where A represents adenine, G for guanine, T for thymine and C for cytosine.

During DNA replication, the two strands dissociate first and on unwinding each DNA chain serves as a **template** for the synthesis of two complementary chains. DNA replication is, therefore, a typically *copy* mechanism. Thus, due to this, two DNA molecules are produced which have exactly the same molecular constituents.

Ribonucleic acid (RNA)—Ribonucleic acid (RNA) is present in the nucleus and cytoplasm. The main role of RNA is in the transcription of genetic information contained in the DNA molecule and also in protein synthesis.

Unlike DNA, RNA in most organisms exists as a single strand, although in several places it may fold back to produce helices as found

in DNA (Fig. 3.10). In this region of helix the bases are hydrogen bounded and the base pairing is typically like DNA although thymine is replaced by uracil and so the pairing of adenine takes place with uracil and guanine with cytosine. In case of RNA the sugar is of ribose type.

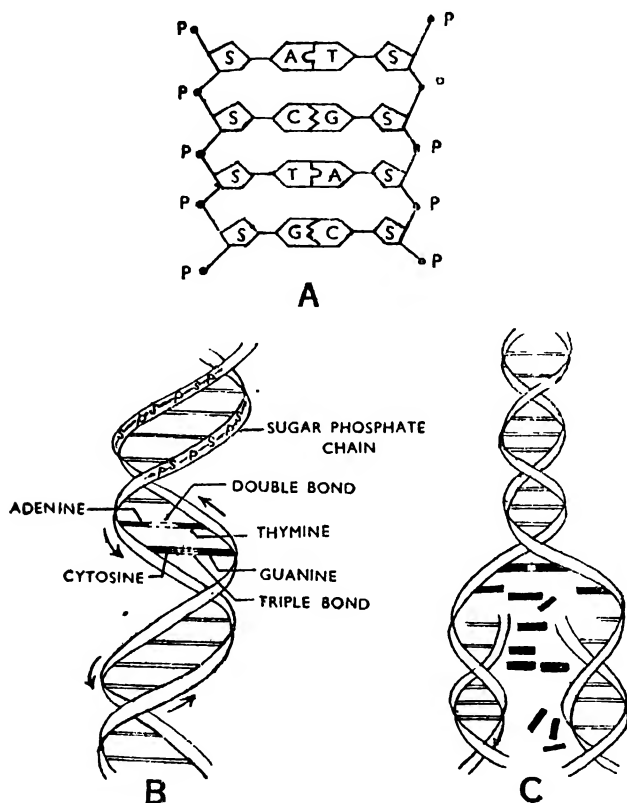


Fig. 3.9 A. Diagrammatic representation of the parts of DNA (P=phosphate S=Sugar, A=Adenine, T=Thymine, G=Guanine, C=Cytosine)
B. Two phosphate sugar chain showing double helical structure of DNA, C. Gene replication

There are three types of RNA present in the cell: *ribosomal RNA* (rRNA), *messenger RNA* (mRNA) and *transfer RNA* (tRNA).

Ribosomal RNA is the major RNA fraction of the cell and constitutes about 80–90% of the total cellular RNA. It is always found to be associated with protein. The combination of ribosomal RNA and protein forms the cellular body known as *ribosome*. The ribosomes consist mainly of two subunits of 30s and 50s. These subunits may unite forming larger complexes of 70s (s=*Svedberg*

unit). In some cases more units may be attached to form a more larger complex of 100s. It is then called a *polysomes*. The ribosomal RNA from different organisms will have different sedimentation constants.

Messenger RNA is the second type of RNA involved in protein synthesis. The base sequence of *messenger RNA* is complementary to that of DNA particularly when the DNA unwinds. The name "messenger" is given as it transcribes the information from the DNA and carrying it to be translated into protein in the cytoplasm. This constitutes about 5-10% of total RNA.

Transfer RNA is also known as *soluble RNA* (sRNA). The main role of transfer RNA is in protein synthesis. Each transfer RNA carries one amino acid molecule to the site of protein synthesis. In addition to its usual bases, the tRNA contains some methylated bases (e.g. methylcytosine, hydroxy methylcytosine. Holley (1965) reported a complete nucleotide sequence of tRNA that is specific for the amino acid alanine.

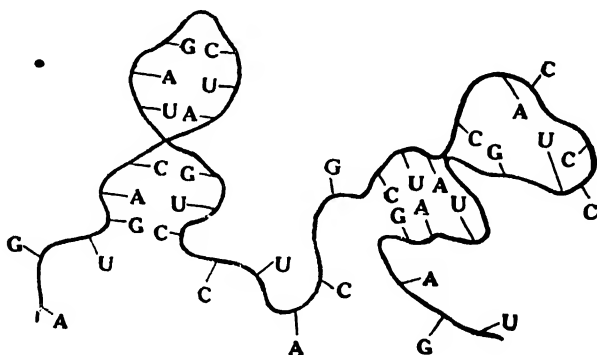


Fig. 3.10 Proposed structure of ribonucleic acid (RNA)

Chemically DNA and RNA have got similarities and differences. As both the nucleic acids contain purine and pyrimidine bases, both of them absorb ultraviolet light and maximum is in the region of 2600\AA . RNA also like DNA stains with basic dyes. Regarding the differences of the two nucleic acids, DNA contains sugar which has got one oxygen atom less suggesting the chemical nature "deoxyribose." In the base composition thymine in DNA is replaced by uracil in RNA.

2. PROTEINS ;—Protein make up the largest part of the chromosome by volume. Among the basic proteins, histones and protamines have been identified from chromosome. Histones are common and found in the nuclei of all higher plants and animals. Protamines are not present in all chromosomes, but were, however, isolated from fish and fowl sperms. An additional residual protein digestible by trypsin but not pepsin, forms the framework of the chromosome.

Histones and protamines are combined with DNA in ionic form, salt linkages are made with the phosphate groups of the nucleic acid.

Among the non-basic proteins, tryptophan is important. Non-histone or residual proteins remain in the chromosome after DNA-histone-complex has been removed. Non-histone proteins are present mostly in the metabolically active cells than the less active cells.

3.4 Chromosome Theory of Heredity—A living being arises from a pre-existing living being and this takes place through reproduction which may be either asexual or sexual. By means of asexual reproduction, a part of the parent body produces new progeny but in case of sexual reproduction male and female gametes play a major role. Between the parent and the progeny there is a physical continuity in both the asexual and sexual type of reproduction which is evident in case of planting of cuttings (i.e. in asexual reproduction).

The physical continuity is not evident in case of sexual reproduction due to small size of the gametes.

After the discovery of the Cell theory by Schleiden and Schwann (1838), it becomes clear that the cell is an important structure from the physiological and hereditary point of view. The nucleus maintains its continuity from one generation to another and is the most important constituent of the living cell.

New cells are formed by means of division which causes the increase in number. From a single cell by division generally two daughter cells are formed and during cell division the nucleus plays a prominent role and undergoes many changes.

Several thread-like bodies are found within the nucleus which were detected by Hofmeister (1848) and Waldeyer (1888). They coined the term "chromosomes" for those thread-like bodies.

That nucleus plays a prominent part in heredity was studied by Strasburger, Hertwig and Weismann.

The chromosomes primarily arise by the division of the pre-existing ones and their number in a cell is permanent. In the inheritance of characters, chromosomes are the most important constituents in the nucleus. Chromosomes are the carriers or genes which are responsible for the development of character in living organisms. From generation to generation the progenies more or less resemble their parents.

All rice plants distributed in the world bear certain similar characteristic features. In general appearance, spikelet inflorescence, internodes with sheathing leaf bases feathery stigmas with caryopsis fruit they resemble grasses and for that reason they are placed under the family Gramineae and because all of them look similar to each other, they are placed under one genus and species—*Oryza sativa*. The different varieties of rice cultivated in the various places of the world are prominent and they differ from each other in few minor characters.

The number of chromosomes within a species is generally constant and from parents to progenies, the chromosomes are received directly.

During sexual reproduction in most higher plants, the male nucleus unites with the female nucleus and therefore nucleus is the main structure which is responsible for the building of characters in the progeny.

The development of sex in *Drosophila* (fruit fly) is due to the presence of sex chromosomes, that is, a pair of unequal homologous chromosomes, termed XY-chromosomes. In somatic cells the male flies show XY-chromosomes and the female flies show XX-chromosomes. Two kinds of gametes are produced by male in equal numbers. One with X-chromosomes and the other with Y-chromosomes. But the female produces one kind of egg, all carry one X-chromosome. After random union, zygotes with XY-chromosomes produce male and the zygotes with XX-chromosomes develop into females.

Each character is presented by a factor in the gamete in case of inheritance. Such characters do not mix with each other on hybridisation but behave independently as separate units. The same characteristics are exhibited by chromosomes and this is termed as *particulate type* of inheritance.

Chromosomes contain some permanent distinct particles which occupy respective position on a particular chromosome. They are called *genes* and are arranged in linear sequence over the chromosome. These are complex protein molecules capable of developing characters.

When a portion of the chromosome is lost due to fragmentation by X-ray treatment, some character or characters fail to appear in the next offspring. This shows that the lost portion possesses some genes which are responsible for the development of those characters.

The offsprings derived by vegetative propagation are all identical in nature while the offsprings derived through seeds show variations.

The characteristics of the progeny are equally shown by the two parents and the zygote contains one haploid complement of chromosome from each parent. The sperm carries a very little amount of cytoplasm but the egg supplies a great amount of cytoplasm.

Thus it is proved that the chromosomes of the nucleus are solely responsible for the gradual growth of *hereditary characters* in the offspring.

Variations in Chromosome Structure or Chromosomal Aberrations

The genes are present in the chromosomes and therefore the hereditary change may occur not only through the change in the number of chromosomes but also through a change in the structure of the chromosome. This change in the chromosome structure may be brought about spontaneously or by experimental accidents. This type of gross change in the chromosome structure is termed as **chromosomal aberration**. The possible cause of such changes may be radiation of different types, nutritional disbalance and environmental changes (e.g. temperature). Although the origin of such changes is not known, but it is believed to be caused by breaks in the chromosome or in the chromatid. The two broken ends may remain *united* causing an eventual loss of that chromosomal segment which does not contain the centromere. The broken ends may immediately unite in the same way thus restitution of the chromosome may occur. The broken end of a particular chromosome may join with another broken part of a different break thus causing an exchange.

Depending upon the number of breaks, locations and the pattern in which the broken ends rejoin, the four possible aberrations are ; *deficiencies or deletions, duplications, translocations and inversions*. This change may involve in the number or arrangement of gene loci within a chromosome.

4.1 Change in number of genes :

1. **DEFICIENCIES OR DELETIONS** :—Deficiency or deletion represents a loss of chromosomal material. It has been observed first by Bridges (1917) in *Drosophila*. This loss may either be from the ends of the chromosomes, when it is termed as **terminal** or the loss may be from the segment of the chromosomes when it is termed as **intercalary (interstitial)**. The deleted segment whether terminal or intercalary does not survive if it lacks a centromere. The terminal deletion involves a single break near the end of a chromosome whereas the interstitial deletion involves two breaks and the four freshly broken ends then reuniting two by two in a new way (Fig. 4.1A). As a result of this break an acentric fragment is formed and the chromosome lacking this fragment is deficient of the genes present in the particular region. Such loss will therefore have a phenotypic effect upon the organism. The deficient regions vary from a very minute sub-microscopic segment to a major portion of the chromosome. If

the deficiency is large, there is a likelihood of a greater genetic effect. If, however, a very large segment is lost the effect is lethal to the cell. In some cases, however, the organisms are able to withstand the loss of an entire chromosome without any significant damage.

During meiosis when this deficient chromosome meets with a normal one, the normal chromosome bows out as an unpaired loop.

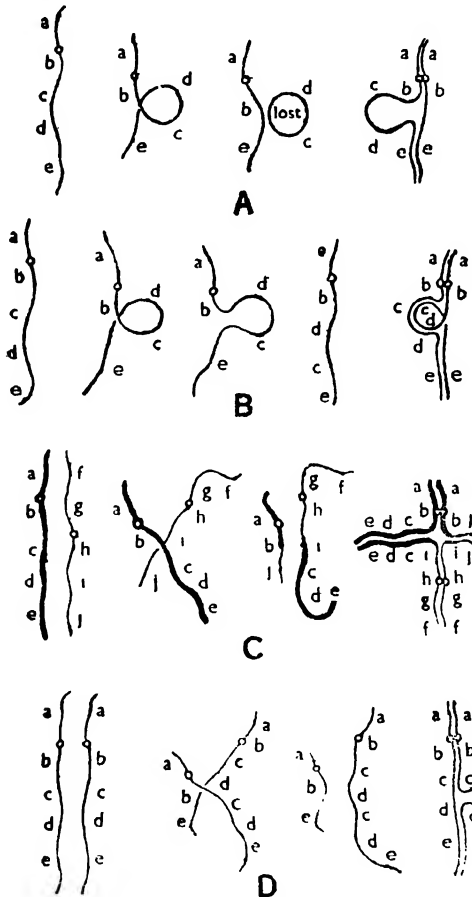


Fig. 4.1 A. Diagram showing deletion B Diagram showing inversion
C. Diagram showing reciprocal translocation occurring between non-homologous chromosomes D. Diagram showing duplication.
In B, C, D the synapsis of the chromosome with normal chromosome

(Fig. 4.1A). Deficiency is important in the determination of gene location in the chromosome.

2. **DUPLICATION** :—When the addition of some part of chromosome to a chromosome takes place in such a way that a section is

longitudinally repeated, the phenomenon is known as **duplication**. The repeated segment may join with one of its homologous chromosomes or to a non-homologous chromosome or it may exist as a small chromosome with its own centromere. Further, the orientation of the repeats may be normal or inverted depending upon the manner in which they are added (Fig. 4.1D).

Since the repeats involve genes, a genetical effect may be produced due to duplication. The well known **bar eye** in *Drosophila* is an extreme example of duplication. Bar is due to the addition of two adjacent segments of the chromosomes, the double bar eye is, however, due to triplication of the genetic locus for the normal eye.

Duplication can be cytologically well observed in the polytene chromosome of *Drosophila melanogaster*. When the added segment is placed in the same homologues and in the same genetic order as the original segment, the duplication is termed as **tandem**. When they are arranged in reverse order in the same homologues, they are termed as **reverse tandem**.

Tandem $\rightarrow ABC\ ABC\ DEF$

Reverse tandem $\rightarrow ABC\ CBA\ DEF$

Displaced $\rightarrow \begin{cases} ABC\ DEF \\ I\ JK\ ABC\ LMN \end{cases}$

In case of displaced duplication the segmented parts are attached to a different chromosome. During meiosis the duplicated chromosome forms a loop whereas the unduplicated one remains straight.

4.2 Change in the arrangement of genes :

3 **TRANSLOCATION** :—Sometimes a part of the chromosomes is detached and re-united to a different part of the same chromosome or to a different chromosome. Such re-arrangements, except by normal crossing over, are called **translocations**.

Generally three types of translocation can be recognised.

(a) **Simple**—It involves a single break in a chromosome and the broken part is transferred to the end of the same chromosome or to another chromosome. But since the normal chromosome end is unable to attach any part of the detached chromosome, simple translocation is of rare occurrence.

(b) **Reciprocal**—A single break in two non-homologous chromosomes produces an exchange of chromosome segments between them (Fig. 4.1C). Such translocation is termed as **reciprocal translocation**. Reciprocal translocation is the most common type of translocation.

(c) **Shift**—It involves three breaks in the chromosome and union of an interstitial portion from its original position to a different position of the same chromosome or to another chromosome. Shift may also be termed as **transposition** (Kaufmann, 1954). Here the

chromosome also involves three breaks and the segment is changed from one position to another. Thus a transposition involves two successive inversions in the same chromosome.

e.g. $ABCDEFGHI \rightarrow ABFEDCGHI \rightarrow ADEFBCGHI$

Here the segment BC is transferred from one chromosome end to another end. It is the common type of translocation.

Translocations do not involve a loss or an addition of chromosome materials but only the re-arrangement of the chromosome segments, and like duplication and deficiencies, it may be either homozygous or heterozygous. Homozygous translocation behaves normally in meiotic division and cytologically not distinguishable but a heterozygous translocation shows variation in the pattern of chromosome pairing during meiosis. An individual with two translocated chromosomes and two normal chromosomes with which

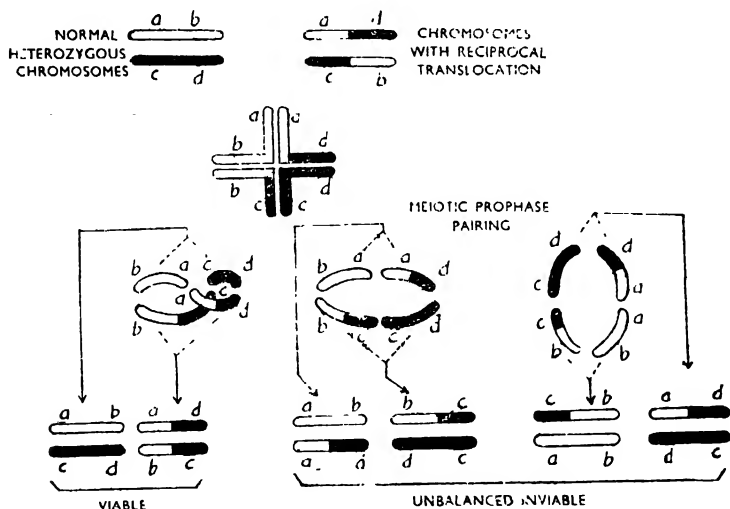


Fig. 4.2 Diagram showing translocation
Chromosomes showing behaviour of heterozygous translocation in meiosis.
Chromosomes from egg and translocated chromosomes from pollen
are represented in meiotic prophase pairing, separation in
anaphase and formation of two viable and four
non-viable gametes

they are homologous is called a structural hybrid. During synapsis of homologous parts they form a cross-shaped appearance (Fig. 4.1 C) and at diakinesis they open out as a ring or chain. Such ring or chain is known as catenation. At anaphase, the chromosomes in the ring may move in two ways : alternate or adjacent. When the alternate member goes to the same pole two types of gametes are produced and since each of them contains all the chromosomal elements, the gametes are functional. In cases where the adjacent

members move to the same pole, four types of gametes are obtained. But here the gametes are nonfunctional as all of them lack certain elements of the chromosome (Fig. 4.2). On selfing, two functional male gametes unite with the two functional female gametes and produce offsprings of three types (i) standard plants with normal chromosomes in duplicate (ii) structural hybrid and (iii) modified plants with translocated chromosomes in duplicate, in the ratio of 1 : 2 : 1.

Translocation is of regular occurrence in plants. Reciprocal translocations have been widely observed in several races of *Oenothera*. Another plant with regular translocation is *Rhoeo discolor*. Some species of *Datura* also exhibit reciprocal translocation.

4. INVERSIONS :—Inversions occur when the sequence of genes are rearranged in a reverse order. If a chromosome undergoes two break at two different loci of its body and if the broken part undergoes rejoining at a reversed position, the result is the origin of an inverted chromosome (Fig. 4.1B).

It is a kind of chromosomal aberration in which a segment of chromosome exists in a reverse relationship to the rest of the chromosome. The linear order of the genes is thereby reversed in a particular chromosome. If the arrangement of the genes in a chromosome be ABCDEFFA and if the inversion occurred between D and F, the inverted chromosome would have a gene sequence of ABCFEDGH. The inversion is called **paracentric**, if the inverted segment does not include the centromere and **pericentric** when the segment includes the centromere. When an identical inversion takes place in homologous chromosomes normal meiotic pairing occurs. If however, one homologue has an inversion another remains normal such pairing in meiotic sequence is remarkable. The normal chromosome corresponding to the inversion forms a loop. The inverted one forms another loop but in a reverse direction.

In the chromosomes that carry paracentric inversion, crossing over results in the dicentric and acentric chromatids. The dicentric chromatids form a bridge and thus interfere with the normal division. So the presence of a bridge is a cytological method for detecting inversions at meiotic cell divisions. In case of pericentric inversion, the chromatids are formed with a deficiency and a duplication. Thus an imbalance of chromosome part results after crossing over. Both the inversions produce unbalanced gametes and non-viable zygotes.

Translocation and inversion do not involve any change in the amount of genetic materials, but only changes in the order of the genes in the chromosomes. Such rearrangements involve change in the phenotypic alteration. Such phenotypic alteration due to rearrangements of genes is known as **position effects**. The well known bar and double bar eye in *Drosophila* is the best example of position effect. Position effect may be due to structural changes in the gene at the point where the break occurs or it may be due to altered chemical environment following rearrangement.

Variations in Chromosome Number or Polyploidy

A normal plant shows in each one of its body cells, twice the number of chromosomes ($2n$) found in the gametes. This doubling is due to the fertilization effected by the union of male and female gametes with equal number of chromosomes (n). Such plants are termed as *diploids*. Thus the whole chromosome set found in the gametes is termed as **genome**. So n represents a genome of a particular species of plant and animal. Chromosomes are carrier of genes and these genes are linearly arranged within the chromosome. It has been pointed out that the genes are comparatively stable, but occasionally mutate. Mutation also includes the changes in the structure of the chromosome. There is another type of change which causes increase in the number of chromosome, in multiples of the haploid number, is termed as **polyploidy**.

There are two main types of chromosomal variation that involve changes in the number. These are **euploidy** (in Greek *eu* means true or even ; *ploid* means unit), which involves the variation of whole sets of chromosomes and **aneuploidy** (*aneu* means uneven) where a single chromosome within a set varies. This variation may be either increase or decrease in the chromosome number. The euploids include diploid ($2n$), triploid ($3n$), tetraploid ($4n$) or even higher degree of polyploidy.

Polyploidy thus involves more than two genomes and is therefore a genometric mutation involving increase in the dose of whole genome. This condition of polyploidy is more common in plants especially in angiosperms whereas in animals it is of very rare occurrence. The main reason for the relative lack of polyploidy in the animals is their sex balance, which is more delicate than that in plants. As it has been pointed out in chapter 12 that intersexes (that means sterility in animals) is the most common phenomenon of any deviation of chromosome number from diploids among animals, only few animals (e.g. salamander, *Artemia salina*) show evidence of polyploidy. Polyploidy has, however, been successfully produced in *Drosophila*. The exact mechanism is however not well understood.

Since this variation in the chromosome number is associated with the phenotypic changes in the organism, so a phenotypic variation is possible. On the basis of this variation the action of individual chromosomes can be identified. Further, variation of chromosome number and character also helps in classifying related species and

they also help in determining their probable origin. Finally, this phenotypic variation (due to increased chromosome number) adds much to their morphological and physiological values which helps them commercially and also in evolution.

TABLE 3
Types of variation in chromosome number

Type	Number	Description
Euploids		
Monoploids	n	genetically hemizygous
Diploids	$2n$	two homologous sets
Polyploids		
triploids	$3n$	three homologous sets
tetraploids	$4n$	four homologous sets
etc.		
Aneuploids		
Hypoploids	$2n-x$	loss of one or more chromosomes
nullisomics	$2n-2$	loss of a homologous pair
monosomic	$2n-1$	loss of one member of a pair
double monosomic	$2n-1-1$	loss of two non-homologous chromosomes.
Hyperploids	$2n+x$	addition of one or more chromosomes
trisomic	$2n+1$	addition of one chromosome of a pair
tetrasomic	$2n+2$	addition of two chromosomes of a pair
double tetrasomic	$2n+2+2$	addition of two chromosomes of two separate pair.

5.1 Euploidy or True Polyploidy : Although euploidy means the multiple of monoploid genome (n), diploid ($2n$) with one genome duplicated is the most common euploid. When in an organism the number of chromosome sets exceeds that of the diploids, thus organisms with three ($3n$), four ($4n$) sets etc. are polyploids. Two fundamental types of polyploids are autopolyploids [i.e., self (auto) increase in ploidy] in which the same chromosome set derived from the same species is multiplied and allopolyploids, which occur when different genomes come from two or more different species by hybridization (Fig. 5.1). In autopolyploid, the same genome is multiplied and addition of no new genes takes place. Allopolyploids on the other hand involves the addition of new genomes and so plays a significant part in evolution. Since both of these involve the increase of whole set of chromosome, it is very difficult to determine whether the polyploids are auto- or allopolyploids unless information from its ancestral history and chromosome studies is available.

Induction of Polyploidy—Polyploidy can be induced due to aberration in cell divisions. This may be occur both in the mitosis as well as in meiosis.

In mitosis, failure to form cell wall after the division of nucleus leads to doubling of chromosome number. If a shoot arises from such a cell, the plant will be tetraploid and if such a failure occurs in

germinal tissue shortly before reduction division, diploid gametes are formed from such cells. This type of irregularity may also occur at anaphase, when the spindle mechanism may fail to separate the sister chromatids to opposite poles. Consequently the chromosome number is doubled.

Failure in *meiosis* produces a diploid gamete instead of a haploid and a chance fusion of such a gamete with other types of gametes produces different types of polyploidy. The chance fusion of two such gametes produces a tetraploid ($4n$) plant.

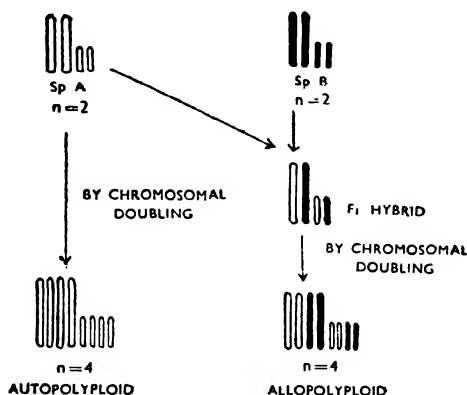


Fig. 5.1 Diagram showing the development of autopolyploid and allopolyploid condition. In the allopolyploid condition, the F_1 hybrid chromosomes are unlike and no pairing occurs. By chromosomal doubling pairing becomes possible.

The triploids containing three sets of chromosomes ($3n$) may arise by various means. Due to failure of normal meiotic division, diploid gametes ($2n$) will be formed. Fertilization between such a gamete and a haploid gamete (n) from the normal diploid plant will result in a triploid ($3n$) form. Triploids may also be formed when an unreduced egg ($2n$) is fertilized by a normal gamete (n) or a haploid egg may be fertilized twice by two haploid sperms (dispermy). Triploids are of quite rare occurrence in plants. Since, though the triploids are viable, the gametes formed are of defective types and so are completely sterile. Normal synapsis between odd number of chromosomes at meiosis is not possible. Pairing will occur with only two homologues at a time, thus the third remains unpaired, thereby forming an univalent. Even, if they pair to form a trivalent, it may be randomly distributed in the gametes. Thus in either of the cases, abnormal gametes will be formed which will consequently fail to fertilize and so sterility will follow. These plants only multiply by asexual methods e.g. chrysanthemum, dahlias, roses etc. Some of the common important varieties of apple, bananas, grapes, oranges etc. are triploids and are propagated vegetatively.

Tetraploids ($4n$) originate by doubling in diploids and may also arise through intercrossing with various polyploids. Tetraploids also result from the duplication of somatic chromosome following mitotic irregularities.

The method of inducing polyploid in plants artificially has been shown by Avery, Blackeslee and Nebel (1937). They have shown that in *Portulaca* and *Datura*, the alkaloid colchicine (extract from the autumn crocus plant, *Colchicum autumnale* (Liliaceae) was very effective in doubling the chromosome number. Colchicine brings about the doubling of chromosome number by acting on the spindle mechanism, and tetraploid plants are produced. Other chemicals like acenaphthene and indole acetic acid (IAA) have also been used for doubling the chromosome number in different plants. Whitkus and Berger (1944) reported another chemical veratrine sulphate which is similar to colchicine in its effect on cell division.

Autopolyploidy :—Autopolyploids may arise by duplicating the same genome in an organism. Presence of more than two sets of chromosomes in autopolyploids results in complex meiosis. During meiosis pairing and crossing over of chromosomes take place between them. Where there are more than two homologues, e.g. three in triploid, four in tetraploid and so in, the pairing between them is difficult, because the meiotic pairing in any region is limited to only two homologues at a time. Thus the third remain unpaired, thereby becoming an univalent. Even if it pairs to form a trivalent, it will be randomly distributed in the gametes, so that some gametes have two homologues and others only one. So a high degree of sterility may be observed. This type of sterility found in triploid holds for all sexually reproducing organisms with an odd number of chromosomes e.g. pentaploids ($5n$), septaploids ($7n$) etc. On the other hand, organisms with even number of chromosomes e.g. tetraploids, hexaploids etc. have a better chance of pairing and an equal separation of chromosomes during meiosis. In autotetraploids of *Datura*, tulip and lotus, gamete formation appears to be normal since an equal separation of chromosome in meiosis occurs in the majority of cases.

Autopolyploidy is of frequent occurrence in plants. The first case of autopolyploidy was noted by de Vries (1901) in *Oenothera lamarckiana*. Other autopolyploid plants are plums, tomatoes, corn, rye and others. Many important commercial varieties of banana, apples and pears are triploids; whereas potato, coffee, peanuts are tetraploids. All these varieties are commercially advantageous than the normal diploid varieties. Because of these desirable features, autopolyploids have now been used considerably in the improvement of many of our commercial varieties of horticultural plants.

Allopolyploidy :—It is derived by doubling the chromosome in hybrids. When a pure diploid species is crossed with another diploid species (sometimes inter-generic), in the cells of the hybrid there is

one haploid complement from each of the parental forms. Since the parental species differ widely from each other, the two haploid compliments of chromosomes in the hybrid are different. During meiosis in such hybrid, the chromosomes lie about as univalents. Separation to the poles at anaphase is irregular and the resulting gametes are non-functional, with the net result that the hybrid is sterile. The sterility is caused by non-homology between chromosomes and non-pairing between them during meiosis. If the chromosome number in such a hybrid is doubled, each chromosome is

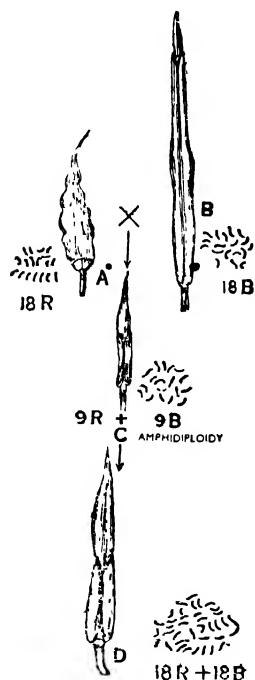


Fig. 5.2 Diagram showing the origin of *Raphanobrassica* (D). *Raphanus sativus* (A) is crossed with *Brassica oleracea* (B) forming sterile hybrid (C)

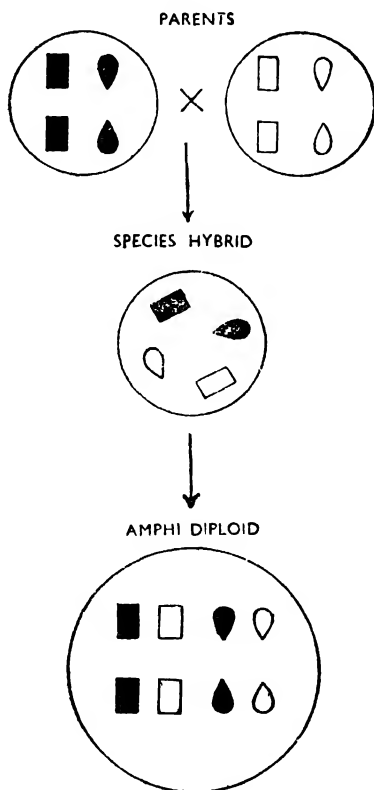


Fig. 5.3 Diagram showing the development of amphidiploid condition

duplicated. Pairing between the duplicated chromosomes is perfect, meiosis is fairly regular and fertility is restored. Such a hybrid in which the chromosome number is doubled is termed as **allotetraploid** or **amphidiploid** (Fig. 5.3).

The **allopolyploid** hybrid combines some of the characters of the two parents and also possesses some distinctive qualitative characters

which differentiate it from either parent. It breeds true and does not cross with the parental species. It is thus, a new species formed suddenly.

An important allopolyploid series is that of wheats. Wheats are of three kinds : einkorn group with 14 chromosomes ($n=7$), emmer group with 28 chromosomes ($n=14$) and aestivum group with 42 chromosomes ($n=21$). It suggests that the three types constitute a polyploid series with diploid, tetraploid, and hexaploid numbers. The commercial American cottons are also allotetraploids ($4n=52$). Similarly, Karpechenko (1927) synthesized an intergeneric allopolyploid *Raphanobrassica* by crossing radish (*Raphanus sativus*) and cabbage (*Brassica oleracea*) followed by chromosome doubling.

Similarly, a number of other cultivated plants are the examples of allopolyploids.

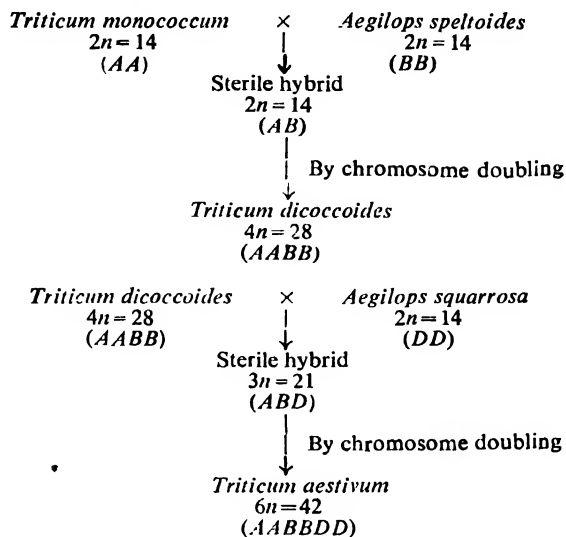
Importance of Polyploids—A study of polyploids is important in the plant hybridization as it offers scope to increase the chromatin content of a cell. Polyploids can bring about quantitative changes in the gene content which can favourably affect the desirable characters in breeding materials. Polyploids also play a great role in the evolution of economic plants and so a knowledge of the process is helpful not only to reveal the relationship between species but also of great significance in the hybridization technique for the improvement of crop plants.

Role of Polyploids in Plant Breeding—When the techniques for artificial chromosome doubling became established, investigations on the origin of many of our economic plants were resumed. Many of our important crop plants like wheat, oat, sugar-cane, cotton, tobacco as well as many fruits and vegetables are the polyploids of various degrees.

Among the cultivated varieties of wheat three different chromosome numbers, are represented : diploid ($2n=14$), tetraploid ($4n=28$) and hexaploid ($6n=42$) with the basic number 7. The primitive small-grained einkorn type (*Triticum monococcum*) has 14 chromosomes in its vegetative cells. It has got very little commercial value. An emmer wheat (*Triticum dicoccoides*) has 28 somatic chromosomes. It has a very thick ear, with large hard kernels and is usually used as stock feed. The bread wheat (*Triticum aestivum*) have 42 somatic chromosomes. Percival (1863-1949) first postulated that the bread wheat came from emmer wheat and goat grass (*Aegilops* sp.). This theory of Percival was however confirmed from the experimental evidences of McFadden (1946), Sears (1948) and others. They have clearly established the idea of origin of bread wheat. According to them the emmer wheat contains two distinct genome (*A* and *B*) and are found to have originated from amphidiploids between *Triticum monococcum* (*AA*) and *Aegilops speltoides* (*BB*).

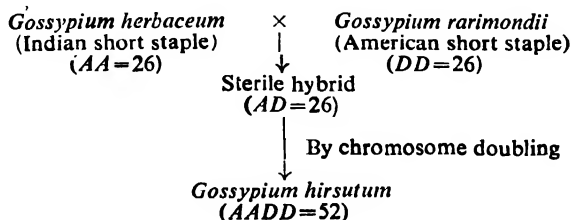
The present day hexaploid wheat (*Triticum aestivum*) arose as a result of hybridization between a tetraploid wheat of emmer group

(*AABB*) and a diploid group (*DD*) of goat grass (*Aegilops squarrosa*) followed by chromosome doubling in the hybrid. The origin of bread wheat is illustrated below :



These experiments indicated that a moderately useful wheat and a useless weed hybridize to produce the man's valuable plant crop, wheat.

Cotton and mustards provide other examples of the role of polyploidy in the production of crop plants. Analysis of possible origin of long staple cotton provides an additional example of polyploidy. Inter specific crosses can be made between two distinct species of cotton. The hybrids show a very wide range of vigour and fertility. Indian short staple (*Gossypium herbaceum*) has 13 pairs of large chromosomes. American short staple (*Gossypium raimondii*) has 13 pairs of small chromosomes. The hybrid, however, is a long staple type (*Gossypium hirsutum*) has 26 pairs, 13 large and 13 small. So the production of a long staple cotton evidently occurred through hybridization followed by chromosome doubling. The cross is shown below :



Similarly there is evidence that the common tobacco (*Nicotiana tabacum*, $4n=48$) is an allotetraploid between *N. sylvestris* ($2n=24$) and *N. tomentosa* ($2n=24$).

Raphanobrassica is an example of experimental compliments of species hybrid. Karpechenko (1927) produced this new species from crosses between two common vegetables belonging to two different genera, the radish (*Raphanus sativus*) and the cabbage (*Brassica oleracea*). Both radish and cabbage had 9 pairs of chromosomes. The hybrids showed 18 chromosomes of which 9 came from radish and 9 from cabbage. The F_1 hybrids are mostly sterile and therefore could not perpetuate itself, due to failure of pairing between the unlike chromosomes in meiosis. By chromosome doubling, however the tetraploid was produced and since two sets of chromosomes were now present, pairing was quite regular. Thus the fertile interspecific hybrid is produced.

5.2 Aneuploidy or Irregular Polyploidy : Increase or decrease in the number of homologous chromosomes is called **aneuploidy**. Organisms with chromosome numbers which are not exact multiples

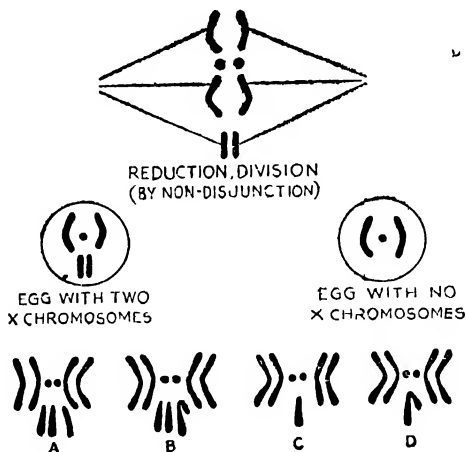


Fig. 5.4 Formation of non-disjoined eggs and corresponding individuals in *Drosophila*. A. Trisomic female, B. Trisomic female (Bridge's experiment), C. Monosomic male (sterile), D. Monosomic dies

of monoploid set (n) are aneuploids. It is the condition in which extra chromosomes are present or some chromosomes are lost. So the two catagory of aneuploids are **hypoploidy** and **heteroploidy**. The former includes the loss of one or more chromosomes ($2n - x$) whereas the latter is defined as the addition of one or more chromosome ($2n + x$). Both these conditions arise due to abnormal distribution of chromosomes during meiosis. This type of abnormal distribution of chromosomes is known as **non-disjunction**, which produces abnormal gametes with extra chromosome ($n + 1$) and some lacking

that chromosome ($n-1$) (Fig. 5.4). Fertilization of such irregular gametes with a normal gamete produces zygotes that have either one extra chromosome ($2n+1$) or lack a chromosome ($2n-1$). Aneuploidy are of the following types.

1. **Monosomic**—It occurs in diploids. Here one chromosome is lost ($2n-1$). Among plants it is usually observed in *Datura*, *Triticum aestivum* and *Nicotiana tabacum*.

2. **Polysomics**—It occurs in diploids. Here one or more chromosomes are added. Trisomic ($2n+1$), Tetrasomic ($2n+2$) etc. are the common examples of polysomics. In the trisomic when all the three chromosomes have the same genetic constitution, it is known as *primary trisomic*. Individuals where the third chromosome is not identical to the other two are called *secondary trisomics*. The most complex trisomic is found in *Datura* and is termed as *tertiary trisomic*, where the trisomic arose by the translocation between non-homologous chromosomes.

Sometimes individuals are produced with two extra chromosomes of the same type and are called **tetrasomic** ($2n+2$). Tetrasomic have been observed in *Triticum aestivum* (wheat).

3. **Nullisomic**—Individual with complete absence of chromosome pair is termed as **nullisomic** ($2n-2$). Serra (1948) first experimentally produced nullisomics types in wheat (*Triticum aestivum*).

The behaviour of the chromosomes in an aneuploid differs extremely from the disomics (normal $2n$) during meiosis and more or less similar to those of polyploids. Like triploids, the trisomics can be expected to produce two types of gametes, one with only one homologue and the other with two.

The first study of aneuploid plants was made by Blakeslee and Belling (1920) in *Datura stramonium*. Trisomic individuals have also been found in *Drosophila*, tobacco and maize. Trisomics also occur in wheat, but due to their similarity in external appearance with normal diploids, they are very difficult to identify. The third homologue in the trisomics interferes with pairing procedure during meiosis. Under normal condition the two homologues pair over their entire lengths producing a bivalent, leaving the third as an univalent. On the other hand a trivalent configuration may occur by the association of all three chromosomes. When the trisomic individuals are mated with normal individuals the genetic ratios are consistent with the expected patterns of segregations and are different from the ratios obtained between the crosses of two diploid individuals. The genetic ratio in offspring of crosses between a normal and a trisomic individual is 2 : 1 or 5 : 1 depending upon the viability of gametes instead of the normal 1 : 1 ratio.

The most important hereditary determiner is the **gene**. Genes are the carriers of information from cell to cell and from one generation to another. They are the unit of inherited material, recognised by their constant effect on the development of any individual bearing them. They are indivisible and highly stable (though occasionally mutates). The exact conception of gene is a matter of large controversy. A number of theories have been put forward to explain the nature of gene. Genes are said to be the *ultimate unit of recombination* i.e. genes are those part of the chromosome between which crossing over might take place. They may also be regarded as the *ultimate unit of mutation* and may be the *unit of physiological activities*. According of Müntzing (1961) genes are "small segment of a chromosome having a unitary biochemical function and a specific effect on the properties of the individual." From the geneticist's view point, however, gene may be defined as *a discrete chromosomal region which is responsible for a specific cellular product and consists of a linear collection of potentially mutable units each of which can exist in several alternative forms and between which crossing over can occur* (Watson, 1970).

Each gene is a part of chromosome. They are made probably of nucleo-protein which is the major constituent of chromosomes. Their size is probably not more than $\frac{1}{10}$ th of a micron. Each gene can construct duplicates exactly like itself from the surrounding materials of the cell. This type of succession of copies of gene takes place during cell division and goes on from one generation to another. A gene is not influenced at all by the other genes which the organism has. Each gene maintains its integrity, but from time to time the structure of the gene alters (during mutation). Every gene has a characteristic effect on development, it affects the development of numerous organs of the individual bearing it. In a constant condition (i.e. constant as regards other genes and environment) a given gene has a constant effect, and often these conditions can be rather widely varied without obscuring the characteristic effects of a certain gene. Possession of a genes therefore makes, in constant conditions, a characteristic difference in an organism, when compared with an allelomorphic gene and that is how genes are identified.

Although genes were first postulated from their end effects expressed in altered phenotypes, they are now known for what they are chemically and for what they can do in directing the development of the individual organisms.

6.1 Chemical nature of gene : Proteins and the nucleic acids are the two most important constitution of genes. Among the

protein histones and protamines make up the largest part, whereas deoxyribose nucleic acid (DNA) is the chemical of which genes of most kinds of organisms are composed. Though DNA was recognised in chromosomes about 75 years ago, but their genetic function was identified only 25 years ago. It is now well believed that the genetic information is carried in nucleic acid molecules.

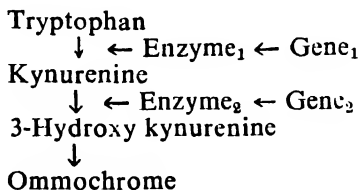
J. D. Watson and F. H. C. Crick (1953) proposed a model for DNA.

For detailed structure of the nucleic acid refer chapter 3, article 3.3. (chemical nature of the chromosome).

6.2 Gene action: The important dynamic problem of whole genetics is how these tiny granules of chromosomes are responsible for the expression of characters.

On the basis of *Neurospora* studies it has been established that genes act through enzymes. One mutant of *Neurospora* could not synthesize the amino acid tryptophan. It was thought that as a result of mutation a single gene had been changed in such a way that the enzyme capable of combining serine and indole to produce tryptophan either was not produced or was inactivated. But on extracting the enzyme from the wild type and mixing it with serine and indole in the laboratory it was possible to produce tryptophan. Thus a direct relationship with gene and enzyme was established. Many other experiments of Srb and Horowitz, Tatum and Beadle led to the *one gene-one enzyme* or *one gene-one primary action hypothesis*. Single specific enzymes were postulated as products of single gene and as agents of specific action.

Gene action can also be well illustrated from the pigments of insects and plants. A classical example of gene action is associated with the eye pigments of insects. Kuhn, Beadle and Ephrussi observed that in the caterpillar the eye colouring pigment is ommochrome. Ommochrome is found to have synthesized from tryptophan (amino acid) through a series of reactions,



All these steps are controlled by specific enzymes which are found to be derived from the specific gene. So if a particular gene is absent or inactivated it can not produce that particular enzyme which is required for a particular chemical step. The consequence is the blockage in the line of reaction and so the final product will not be formed.

Pigment production in flowers, as well as the pigment (melanin)

formation in man apparently follows the same principle of gene-controlled pathways as that in insects.

So the central dogma of gene activity be represented as,

DNA \rightarrow mRNA \rightarrow Proteins \rightarrow Enzymes \rightarrow Characters

6.3 Characters of genes :

(a) *Chromosomal unit* : The ultimate control over the biochemical activities of the cell is exerted by the hereditary determinants or the genes, which in the cells of the higher organisms are incorporated as part of the structure of the chromosome. With these gene the chromosome of the living organisms are said to be formed.

(b) *Specific self duplication* : It is one of the most important property of DNA. Thus is a basic reproductive process that provide a means for living things to perpetuate themselves. The genes replicate during cell division and separated to new cells thus maintaing a genic balance.

(c) *Produce specific effect* : The genes acts as a template for the production of more genes and protein synthesis in the cell. Most known proteins are enzymes which carry out specific functions directed by genes.

(d) *Unit of mutation* : Formerly it was believed that genes are quite stable and cannot undergo any change. But it has now been proved that the genes are changed or can be changed by some agents which directly act on the chemical entities of the gene. These changed structure obviously alter the phenotypic character (mutation) of the organism. The smallest amount of DNA that is effective in causing a mutation is called a muton. Genes are therefore the unit of mutation.'

Mendelian Principles

The new science of genetics was first propounded by Gregor Johann Mendel in the year 1866. He is said to be the “father of genetics”. His conclusion is the basis in the foundation of the modern science of genetics. While he was a monk at Augustinian monastery, in the house of St. Thomas or Königs-kloster at Bränn, Austria (now in Czeschoslovakia), he began his famous experiments on peas (*Pisum sativum*) in the monastery garden in 1857. The results of his experiments were published in the annual proceeding of the Natural History Society of Bränn which appeared in 1866. Mendel’s work which we now define as “Mendel’s laws” is a classic in biology for its elegance and simplicity. With great accuracy, care and objectivity, Mendel conducted his experiments, carefully counted the plants resulting from such crosses and kept statistical records of successive generations with the accuracy of a mathematician.

Unfortunately none of Mendel’s contemporaries thought that he would become famous and nothing was written about him and so his work is completely ignored by the scientists of that time. Another reason for such a neglect may be that the biologists at the time of Mendel were unable to understand or appreciate the statistical approach.

In 1900, long after the death of Mendel, Hugo de Vries, a Dutch biologist, Correns, a German botanist and Tschermak, an Austrian botanist, approached Mendel’s principles independently from their own studies. They incidently rediscovered the laws of Mendel, but with the true scientific spirit they honoured the all but forgotten monk and these laws were called as *Mendel’s laws*.

Although Mendel concentrated his work mainly on peas, the laws apply not only to the garden peas but to other plants and animals as well.

Mendel chose garden pea (*Pisum sativum*) as his experimental material as the plant is easy to cultivate and moreover they are annual in nature. Further, the plants had many well defined inherited differences. Mendel chose seven such different “unit characters” to follow inheritance ranging from stem size to shape of seed. The following are the characters selected and studied by Mendel :

1. Seed shape : either smooth or wrinkled
2. Cotyledon colour ; yellow or green
3. Seed coat colour : coloured with purple flowers or colourless with white flowers
4. Pod type : either hard or soft

5. Pod colour : green or yellow
6. Position of flower : axial or terminal
7. Stature : tall or dwarf

Each character had its two alternative appearance or "traits". Such contrasting pairs of different characters are known as **alleles** or **allelomorphs**. Moreover, pollination can easily be controlled in this plant. Normally the plant is self fertilizing and cross pollination does not occur to any great extent in nature, but artificially they can easily be done. Good fortune as well as the wise judgement marked the selection of garden pea as his experimental material. In his experiment Mendel observed that one manifestation was dominant over another well defined contrasting trait.

Mendel did not originate hybridization but his predecessors in hybridization mainly considered the organism as a whole and studied the inheritance of all the characters at once. But Mendel was the first to consider the result of one trait at a time. When the behaviour of single trait was established, he considered two characters together and in all these cases he actually counted and classified the peas resulted from the crosses with a very great accuracy. Actually his critical mind was a great asset in this line.

Further, the selection of the garden pea was a fortunate one. The selection of characters with which Mendel worked was equally fortunate as they showed complete dominance.

The most important of all these factors is the simple luck which smiled upon him.

MENDEL'S EXPERIMENTS :

7.1 Monohybrid Experiments : Mendel tested individually the seven characters and performed crosses for his experiments with each pair of traits. Thus he crossed a variety carrying a particular trait with another variety carrying its contrasting trait. In this experiment the hybrid possesses a single pair of characters and is known as *monohybrid experiment* or *monohybrid cross*.

Mendel crossed a tall variety of pea with a dwarf variety and he obtained all tall plants. Similarly, in a cross with a variety containing round seed (smooth) with that of a variety containing wrinkled seeds, all plants were found to bear round (smooth) seeds. Thus the initial cross between two varieties is called the **parental** or **P generation** and their offspring is termed as **first filial** or **F₁ generation**. Succeeding generations resulting from this cross are termed as **F₂ generation**, **F₃ generation** and so on.

In all such crosses between two different varieties for each character Mendel uniformly obtained in the **F₁ generation** all plants of only one type. When however, these **F₁ plants** are crossed among themselves, the missing trait appeared again. For example, in a total number of 1064 plants, 787 were tall and 277 were dwarf. Similarly, out of 7324 seeds, 5474 were round (smooth) and 1850

were wrinkled. Therefore in all these experiments the ratio is very close to 3 : 1 or 75 percent : 25 percent.

From all the above crosses of Mendel, three following important consideration can be deduced :

- (1) from a cross between two different varieties, the F_1 plants showed only one trait.
- (2) whatever may be the parents, the reciprocal cross¹ showed always the same result.

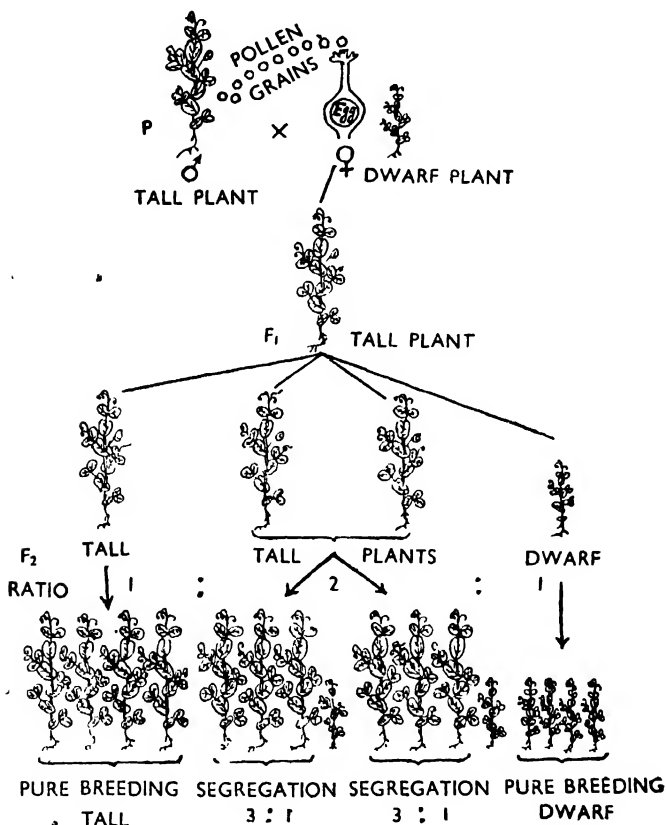


Fig. 7.1 Monohybrid experiment by Mendel showing the result obtained in tall and dwarf cross

- (3) the trait which remained 'hidden' in the F_1 generation, reappeared in the F_2 generation with a frequency of only $\frac{1}{4}$ of the total number.

¹ It is a second cross between the same strains but they carry sexes opposite to the first cross. As for example, a female strain A \times a male strain B and a female strain B \times a male strain A are reciprocal crosses.

Mendel called this determining agent as a "factor". Thus the trait which appears in the F_1 generation, even though the other trait is present, is known as dominant and its alternative is known as recessive. Symbolically, we use capital letter for the dominant trait and the corresponding small letter for recessive of that particular trait. Thus T stands for tall and t for dwarf, similarly S for smooth and s for wrinkled.

Using these symbols, Mendel's experiment can be represented as¹ :

P	TALL × DWARF	
	(TT)	(tt)
gametes	T	t
F ₁	Tall (Tt)	
	Tall (Tt) × Tall (Tt)	
	T	t
gametes		
T	TT Tall	Tt Tall
t	Tt Tall	tt Dwarf
F ₂		

SUMMARY CHART

Phenotype	Genotype	Genotypic frequency	Phenotypic ratio
Tall	{ TT Tt }	{ 1 2 }	3
Dwarf	tt	1	1

In the above experiment the tall parent from a variety that produced only tall plant carried one factor which we call the 'gene' for tallness (TT); whereas the dwarf parent had another recessive factor for dwarfness (tt). In the cross both tall and dwarf produce only one kind of gamete, tall parent produces gametes which bear only one gene (T) and the dwarf parent carries only one gene (t). The fertilized egg of such a cross therefore, must have one gene of each kind (Tt). But since T is present and T is dominant over t , the F_1 plants were all tall. Now on selfing two such F_1 plants, the two factors are separated out or segregate from each other in the gametes i.e. there are two kinds of equally frequent pollen and two kinds of equally frequent egg. At the top of the checkerboard two gametes from the female plant are placed. At the left two gametes from the male plant are represented. Checkerboard is mainly a geometrical device for bringing together all possible combinations in the formation of zygotes. The random combination of these gametes

¹ In the cross the female or seed parent is always written first.

to form four zygotes is given in the above diagram. So this gives a proportion of 1 : 2 : 1 corresponding to 25 percent of plants are pure tall (TT), 50 percent with hybrid tall (Tt) and 25 percent with pure dwarf.

To confirm this experiment the F_1 plants were crossed back to the recessive (dwarf) variety, (this is known as *back crossing*), half of the progeny were tall and the other half dwarf. This explains that the F_1 hybrids produce two types of gametes in equal number.

Some special terminology should be cleared to explain the phenomena of different crosses. The factor which controls the character, we call now as **gene** when remain in pairs designate zygotes. Two such individual genes in a particular gene pair are known as **alleles**, an abbreviation of **allelomorph**. An allele of a particular gene is its partner gene. So T is allele of t and *vice versa*. Members of the gene pairs are represented separately in each gamete. Circles are placed around the gametes to identify mature germ cells. When the gene pair contains two identical alleles i.e. T and T , the organism is termed as **homozygous**. When, however, two different alleles are present in a single gene pair, the organism is termed as **heterozygous**.

In 1911 Johansen proposed the term **phenotype** for the visible characteristic of the organisms. The **genotype** defines for the genetic materials that an organism inherits from its parents. For example, in the F_2 generation of the above cross the tall and the dwarf plants are produced in the proportion of 3 : 1 which is incidentally the phenotypic ratio of the cross. In the genetic constitution however, there are three different genotypes 1 TT : 2 Tt : 1 tt . So in all such crosses the phenotypic and genotypic mendelian ratios are 3 : 1 and 1 : 2 : 1 respectively. In the backcross the phenotypic and genotypic ratios are same i.e. 1 : 1.

The following are the principles propounded by Mendel from his monohybrid experiments :

1. *Existence of unit characters*—In the hybrid F_1 generation, the zygotes formed by the two gametes of the parental plants, two units of characters come and lie side by side. They remain quite independent from each other without losing their individual identities.

2. *Dominance*—From each parent one unit character comes in the F_1 hybrid zygote and lie together. One of the two character units shows itself, called *dominant* while the other remains concealed called *recessive*.

3. *The principle of segregation*—Two types of gametes will again develop from the hybrid plant. In the next generation those gametes will unite to form zygotes. In the F_1 hybrid plant, the zygote contains two unit characters which do not mix but lie side by side. In the F_2 generation the plants will be hybrid as well as parental types. The hybrid type breaks down into parental and hybrid types—this phenomenon is known as *segregation*. This is also called *First Law of Mendel*.

7.2 Dihybrid experiments : Mendel performed his dihybrid experiments by taking two pairs of allelomorphic characters. He

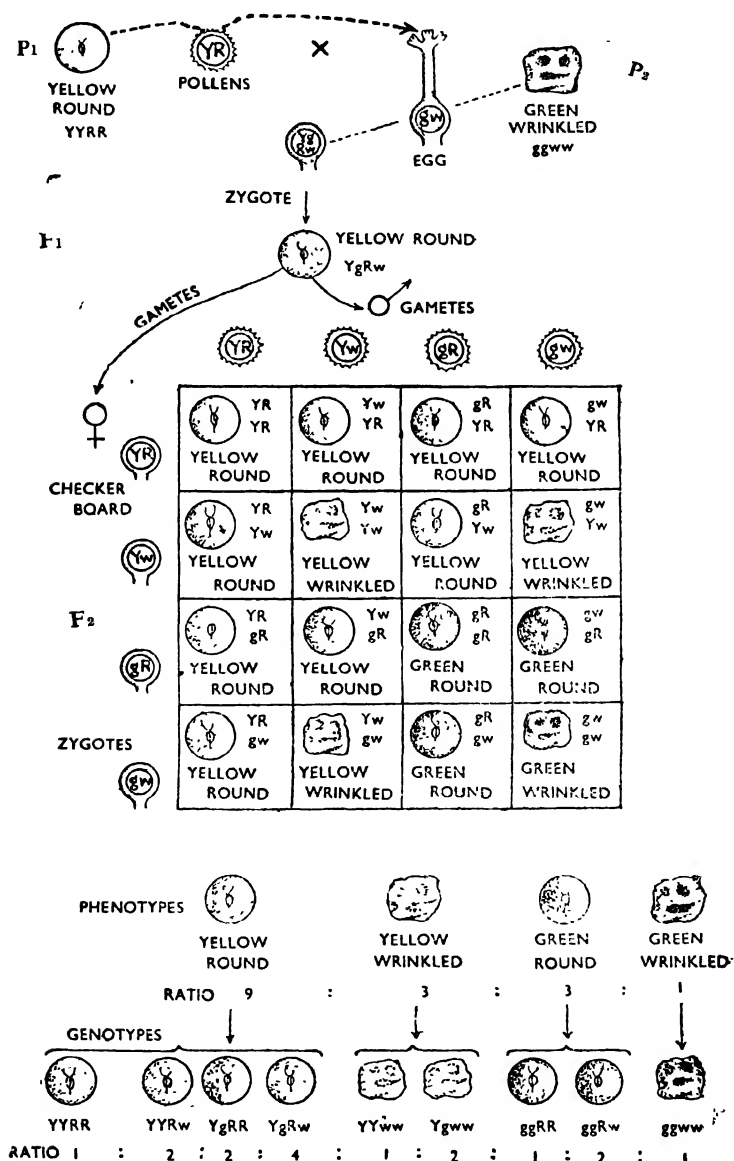


Fig. 7.2 Dihybrid experiment of Mendel showing dihybrid ratio by means of a checkerboard

crossed a variety of garden pea having round seeds and yellow cotyledons with another variety having wrinkled seeds and green cotyledons and obtained the *dihybrid ratio*.

As yellow cotyledon was dominant over green cotyledon and roundness over wrinkledness, Mendel observed all F_1 plants with yellow cotyledons and round seeds. When the F_1 plants are selfed, four kinds of gametes were produced by the female parent and four by the male parent. The possible combination of these gametes to form zygotes is shown in the checkboard (Fig. 7.2). When the results are collected, 9 : 3 : 3 : 1 phenotypic ratio becomes apparent.

It is evident from the above cross that 9 yellow round, 3 yellow wrinkled, 3 green round and 1 green wrinkled seeds were produced. From the external appearance there are four kinds of seeds but from the genetic point of view they are of nine kinds. The complete summary chart is represented below :

SUMMARY CHART

Phenotypes	Genotypes	Genotypic ratio	Phenotypic ratio
Yellow round	YYRR	1	9
	YYRw	2	
	YgRR	2	
	YgRW	4	
Yellow wrinkled	YYww	1	3
	Ygww	2	
Green round	ggRR	1	3
	ggRw	2	
Green wrinkled	ggww	1	1

The result of the dihybrid cross shows that the ratio fit close to the ratio expected if two monohybrid crosses were carried out in the same plant at the same time and so we find that each gene pair acts independently of the other. It means that the chances to be yellow and green do not interfered with or are *independent* of its chances to be smooth or wrinkled. The result shows that not only the pairs of alleles segregate, but also one pair behave independently with respect to another pair. Thus Mendel came to the conclusion that the different pairs of alleles *independently assort* themselves and segregate from each other. This concept is sometimes referred to as *Mendel's second principle* or the **law of independent assortment**.

7.3 Trihybrid experiments : By considering three pairs of characters, Mendel performed his *trihybrid experiments*. The result obtained for dihybrid crosses and those expected for independent assortment was also true for trihybrid crosses. In this experiment Mendel chose three gene pairs, yellow and green seed colour (Y and g), round and wrinkled seed (R and w) and violet and white flowers (V and v). In all the character pairs the first factor is dominant. Then, when the crossed yellow-round-violet plant ($YYRRVV$) with green-wrinkled-white plant ($ggwwvv$) ; he obtained F_1 plants all of

which have a phenotype of the dominant parent ($YgRwVv$). When the F_1 plants were selfed, eight kinds of gametes were produced from both male and female parents. So like dihybrid, each of these gametes has an equal chance of combining with any other gametes thereby producing $8 \times 8 = 64$ expected combinations. Out of these combinations eight phenotypes and twenty seven genotypes were produced in the following ratio.

27	Yellow-round-violet	(8 genotypes)
9	Yellow-round-white	(4 genotypes)
9	Green-round-violet	(4 genotypes)
9	Yellow-wrinkled-violet	(4 genotypes)
3	Green-round-white	(2 genotypes)
3	Yellow-wrinkled-white	(2 genotypes)
3	Green-wrinkled-violet	(2 genotypes)
1	Green-wrinkled-white	(1 genotype)

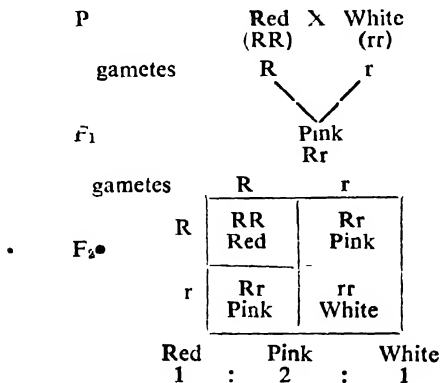
Because of dominance only 8 different phenotypes were produced and since some phenotypic effects are produced by more than one genotype, the number of different phenotypes is always less than the number of genotypes.

From all these experiments one important question is how frequently should the various combinations be expected to occur in succession? The answer lies with the law of probability, i.e., if two or more events are independent the chance that they will occur together is the product of their separate probabilities. As for example when a single coin is tossed, the chance of heads occurring twice in succession would be $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. Similarly the chance of three such occurrences would be $\frac{1}{8}$ and four $\frac{1}{16}$. Next question concerns the goodness of fit of the results obtained from an actual cross when compared with a hypothetical ratio. (For detail refer *Biometry* portion).

7.4 Present status of Mendel's Theory : Since Mendel, additional data began to accumulate and extensive studies have been made by different scientists from all corners of the world. With the gradual advancement of science and with the accumulation of more accurate information, it is evident now that a single gene is not responsible for the expression of a single trait, which is the major basis of Mendel's work. It is now believed that all the genes present in an organism affect the expression of a trait in some way or other. According to the recent information, several genes influence the same basic reaction and so are responsible for the altered characters or phenotypes. In the heredity, it is the genes and not the trait which are inherited generation after generation. Genes behaves as independent units whereas the traits are the end result of complex interaction involving several genes.

Experiments with diverse plants and animals clearly indicate that the Mendel's basic principle of dominance and the principle of independent assortment does not hold good. Although the principle of segregation remains unchanged even today.

Mendel in his experiments clearly indicates that dominance is an inherent property of genes. One trait of the allelomorphic pair is expressed whereas the other remains suppressed. The question of complete dominance remain same in all the seven character pairs which Mendel reported. There are many cases where the hybrid individuals are more or less intermediate between the parents. Thus when the homozygous red and white variety of 4 o'clock plant (*Mirabils jalapa*), snapdragon (*Antirrhinum*) and sweet pea (*Pisum sativum*) are crossed, F_1 plants are all pink flowered. The F_2 generation consists of red, pink and white in the ratio of 1 : 2 : 1. The red and the white flowers breed true whereas the pink again segregate into 1 : 2 : 1.



The homozygous RR and rr gives red and white flowers respectively. The heterozygous Rr gives pink as both R and r have about equal effect, there being no dominance of the one over the other. Here the genotypic and phenotypic ratio are same. Therefore Mendel's view on dominance is no longer tenable for all cases.

The most important idea of Mendel is that of the independent combination of different pairs of alleles. But the post mendelian work simply goes against the law of independent assortment. Although Mendel was aware of this type of irregularities, but he did not attempts to clarify it. It has been shown to-day that a number of characters are inherited together rather than independently. The characters which are inherited together are said to be 'linked' and his phenomenon is known as "linkage". (For detail refer chapter linkage). A group of characters that are linked together and are inherited together as a single unit comprise what is called linkage group.

At the time when Mendel performed his experiments knowledge about the structural and functional biological unit, the cell, was meagre. Knowledge about cell division and also sequence of development of reproductive units in the plant was entirely lacking. Without such basic things it is impossible to appreciate the significance of Mendel's experiments.

Interaction of Genes or Factor Hypothesis

Although the Mendelian principles were rediscovered and confirmed in 1900 but these principle were not all valid and applicable in all organisms. Some exceptions are found to occur which deviates from the Mendelian ratios e.g. 3 : 1, 9 : 3 : 3 : 1 etc. This can be explained by assuming that many characters are influenced by two or more pairs of genes located on different pairs of chromosomes which interact in some complex fashion to produce a single trait. In this case one pair may suppress or express the effect of another pair. This is called as **gene interaction** or **factor hypothesis**. The unit particles (genes) or factors are situated on the chromosomes separately, but the combined effect of the genes (in which a number of genes interact) produces the expression of a character. A few such modifications depending upon interaction are described below:

8.1 Incomplete Dominance or Blending Inheritance : Soon after the rediscovery of Mendel's laws, experiments were conducted with thousand of plants and animals to test Mendel's conclusion. But it has been observed from the cases investigated that all did not conform to the principles of dominance. When the dominant factors cannot completely suppress the recessive but the expression becomes intermediate between the two characters, the phenomenon is known as **blending inheritance** or **incomplete dominance**. The familiar example of such an inheritance is the flower colour or *Mirabilis jalapa*. When a red-flowered variety is crossed with a white-flowered variety of four O'clock plant, all the F_1 plants are pink-flowered. The F_2 consists of red, pink and white in the ratio of 1 : 2 : 1.

	Red RR	× ↓ Pink Rr	White rr	
				F_1
	Male gametes	R	r	
Female gametes	R	RR Red	Rr Pink	F_2
	r	Rr Pink	rr White	
F_2 ratio		1	2	1
		red	pink	white

Here both the genotypic and phenotypic ratios in the F_2 generation are same. The red and the white breed true while the pink again produces three kinds of offsprings,

Similar cases also occur in sweet pea and Snapdragon (*Antirrhinum majus*) and in a number of crop plants like cotton, rice etc.

Where both the characters in a dihybrid cross are completely dominant the ratio of the F_2 generation is 9 : 3 : 1. But when in a dihybrid cross, one character shows complete dominance and the other shows incomplete dominance, the F_2 ratio is modified and six phenotypes in the ratio of 3 : 6 : 3 : 1 : 2 : 1 have been observed. In rice, lax panicle (*S*) is dominant over dense panicle (*s*) giving a typical 3 : 1 ratio in the F_2 . Another character clustered spikelets (*C*) is incompletely dominant over non-clustered spikelet (*c*) giving a phenotypic ratio of 1 (clustered) : 2 (intermediate) : 1 (non-clustered).

In crosses involving both these characters the F_1 plant having the genotype *Ss Cc* has lax panicle with intermediate cluster of spikelet.

		Lax panicle cluster SSCC		×	Dense panicle non cluster sscc			
		↓						
		Lax panicle intermediate cluster SsCc						F ₁
Male gametes		SC	Sc	sC	sc			
Female gametes	SC	SSCC	SSCc	SsCC	ScCc	F ₂		
	Sc	SSCc	SScc	SsCc	Sscc			
	sC	SsCC	SsCc	ssCC	ssCc			
	sc	SsCc	Sscc	ssCc	sscc			
Genotypic ratio		Phenotypic ratio						
SSCC	1)	3	Lax panicle, cluster					
SsCC	2)							
SSCc	2)	6	Lax panicle, intermediate cluster					
SsCc	4)							
SScc	1)	3	Lax panicle, no cluster					
Sscc	2)							
ssCC	1	1	Dense panicle, cluster					
ssCc	2	2	Dense panicle, intermediate cluster					
sscc	1	1	Dense panicle, no cluster					

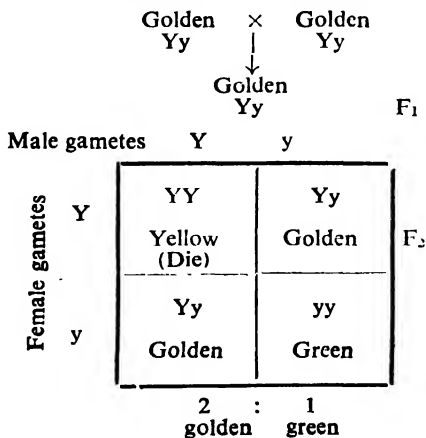
In Snapdragon where both the characters show incomplete dominance, in the F_2 generation of such cross the genotypes and phenotypes are of equal number ; there being nine different genotypes and nine phenotypes. The ratio of such cross 1:2:1:2:4:2:1:2:1,

8.2 Lethal Factor (2 : 1) : The effect of the genes in some cases is so severe that the normal development of the individual is changed and even unable to survive. These are called **lethal genes**. When the effect of the lethal genes is dominant and immediate, the individuals carrying the genes will die. In some cases the effect of the dominant genes is delayed and so the individuals survive for a considerable period. The effect of the recessive lethals can, however, be expressed when there is a chance mating of a heterozygous individual with a carrier partner.

In 1905, Cuenot first reported the inheritance of body colour of mouse and observed that the inheritance of yellow colour usually did not fit with the usual Mendelian pattern. By backcrossing he observed that all yellow mice were heterozygous and no homozygous yellow could be found. According to him yellow had a dominant phenotypic effect and at the same time a recessive lethal, so the homozygous yellow mice were non-viable.

Baur at about the same time observed similar lethal genes in plants. A variety of snapdragon (*Antirrhinum majus*) is known as 'golden' as it bears variegated leaves. When two plants of the 'golden' variety are crossed they give golden and green offsprings in the ratio of 2 : 1 instead of usual 3 : 1. The green offsprings breed true but the golden variety again segregates into a mixed progeny. This clearly suggests that the golden variety is heterozygous. The homozygous plants are entirely yellow and are unable to make chlorophyll. So the homozygous variety straightway perish for want of chlorophyll before germination or at the seedling stage.

In majority of plants, chlorophyll deficiency is also due to the effect of lethal genes. In pearl millet (*Pennisetum typhoides*) the green and albino seedlings were produced in the ratio of 3 : 1. The albino condition is due to the recessive gene (*cc*) and the seedlings will die in a few days after germination. Similarly in cholam (*Sorghum caudatum*) a recessive lethal green can thus be explained.



Several diseases in man which are fatal at different stages of development are due to lethal genes.

8.3 Simple Interaction or two factor pairs effecting the same character : When two pairs of factors affect the same character among two dominants, an interaction occurs to produce a new type, the phenomenon is known as simple interaction and in this case the same characters are influenced by two genes and a variety of phenotypic ratios may appear.

Bateson and Punnett explained this type of inheritance from the study of comb types in fowls. The *rose* and *pea* types of combs are due to two dominant factors in separate chromosomes and *single* comb is recessive to them. The combination of two dominant factors for both rose and pea results in a different type of comb, *walnut*. So it is evident that two different genes interact to give walnut types when the dominant alleles are present and give single combs when both gene pairs are in a homozygous recessive condition.

When a rose-combed fowl was crossed with a pea-combed fowl, a new comb form was obtained in the F_1 generation called walnut. Crosses between walnuts gave four phenotypes in the ratio of 9 : 3 : 3 : 1 each with uniquely distinct comb shape.

		Rose RRpp	×	Pea rrPP		
		↓		Walnut RrPp	F_1	
Male gametes		RP	Rp	rP	rp	
Female gametes	RP	RRPP Walnut	RRPp Walnut	RrPP Walnut	RrPp Walnut	F_2
	Rp	RRPp Walnut	RRpp Rose	RrPp Walnut	Rrpp Rose	
	rP	RrPP Walnut	RrPp Walnut	rrPP Pea	rrPp Pea	
	rp	RrPp Walnut	Rrpp Rose	rrPp Pea	rrpp Single	

The ratio is $\frac{9}{16}$ (walnut) : $\frac{3}{16}$ (rose) : $\frac{3}{16}$ (pea) : $\frac{1}{16}$ (single)

8.4 Epistasis (12 : 3 : 1) : When a gene or gene pair masks the expression of another non allelic gene, the phenomenon is termed epistasis and the gene which produces this effect is known as epistatic

and the gene whose expression is prevented is termed as **hypostatic**. Since the epistatic genes inhibit the expression of other genes they are also called inhibiting genes. In this case two different genes affect the same part of the organism, the expression of one prevents the expression of the other.

This type of suppression is very much analogous with simple dominance. But this should be distinguished from the simple dominance by the fact that epistasis involves non allelic genes whereas dominance is concerned only with alleles. In case of epistasis, two or more genes affect the same part of the organism. One of them is expressed and the other is suppressed so that in modified ratios the original traits are obtained.

The most epistatic effects are associated with colour patterns in plants and animals. In squash (*Cucurbita pepo*) there are three fruit colours : yellow, green and white. The yellow colour due to gene *Y* is dominant to green which is due to its recessive. White colour is due to gene *W* and is dominant to gene *Y*. So, when *W* is present, the fruit will be always white, irrespective of the presence of other colour of genes. In the absence of *W*, the colour of the fruit will be yellow or green, depending on the presence or absence of *Y*.

So, when a white variety (*WWYY*) of squash is crossed with a green variety (*wwyy*), the F_1 offsprings are white fruited with the genotype *WwYy* and in the F_2 generation white, yellow and green fruited plants appear in the ratio of 12 : 3 : 1. The results are shown below :

		White WWYY		×	Green wwyy			
				↓	White WwYy			
								F ₁
		Male gametes		WY	Wy	wY	wy	
Female gametes	WY	WWYY White	WWYy White	WwYY White	WwYy White			
	Wy	WWYy White	WWyy White	WwYy White	Wwyy White			
	wY	WwYY White	WwYy White	wwYY Yellow	wwYy Yellow			
	wy	WwYy White	Wwyy White	wwYy Yellow	wwyy Green			

The ratio is $\frac{12}{16}$ (white) : $\frac{3}{16}$ (yellow) : $\frac{1}{16}$ (green)

The grain colour of cholam (*Sorghum caudatum*) and millet (*Sorghum vulgare*) can also be explained by the above method and in all the cases the coloured genes are hypostatic.

8.5 Complementary Factor (9 : 7) : When two pairs of factors affect the same character with the individual having the same visible effect and their interaction produces a different effect, the phenomenon is known as complementary factor. The sweet pea cross was the first clear illustration of two gene pairs "complementing" each other on their effect on the same trait. Bateson and Punnett observed that when two white-flowered varieties of sweet peas were crossed, the F_1 plants were all found to be purple-flowered. The offsprings of two F_1 plants appeared in the 9 (purple) : 7 (white) ratio. These results clearly suggest that the formation of anthocyanin pigment depends on two independent factors, both of which must be present to produce purple colour, neither by itself can produce the colour.

Thus when the two white-flowered sweet peas, with the genotypes $CCpp$ and $ccPP$, were crossed, all F_1 plants are purple-flowered. Here the gene C produces a colour base and the another gene P activates the colour base to produce colour. The results of the cross are given below :

		White $CCpp$	\times	White $ccPP$		
		\downarrow		Purple $CcPp$		
				F_1		
Male gametes		CP	Cp	cP	cp	
Female gametes	CP	$CCPP$ Purple	$CCPp$ Purple	$CcPP$ Purple	$CcPp$ Purple	F_2
	Cp	$CCPp$ Purple	$CCpp$ White	$CcPp$ Purple	$Ccpp$ White	
	cP	$CcPP$ Purple	$CcPp$ Purple	$ccPP$ White	$ccPp$ White	
	cp	$CcPp$ Purple	$Ccpp$ White	$ccPp$ White	$ccpp$ White	

The ratio is $\frac{9}{16}$ (purple) : $\frac{7}{16}$ (white)

Besides sweet peas, numerous complementary effects between genes have been observed. The aleurone colour in maize is due to this type of interaction. The aleurone in maize can have a variety of

colours, depending on the presence of anthocyanin pigment. As in the case of sweet peas, the appearance of kernel colour in maize depends on a complementary effect between different gene pairs.

8.6 Supplementary Factor (9 : 3 : 4): Of the two independent pairs, one dominant produces its effect whether the other is present or not, but the second can produce its effect only in the presence of the first. Such interaction is termed as **supplementary factor**.

This is also an example of epistasis where the absence of colour is illustrated in mice. This is also known as **recessive epistasis**. The glume colour in millet in general can also be explained by 9 : 3 : 4 ratio. The glume colour inheritance in millet is due to interaction of two dominant factors *P* and *B*. The black purple colour (*P*) is dominant over brown (*p*). The factor *B* present in separate chromosome has no effect by itself or in the presence of the recessive factor *p* but can express itself only in the presence of dominant *P*. The recessive factor *b* has got no phenotypic effect. So when *P* and *B* are present, black purple colour is changed to red. So when a black purple (*PPbb*) was crossed with a brown (*ppBB*) the F_1 plants were all *PpBb* and red glumed.

When these F_1 plants were crossed, their F_2 progeny were classified as 9 (red purple) : 3 (black purple) : 4 (brown). This type of ratio is definitely due to independent combination and interaction of two separate pairs of alleles. The cross is illustrated below :

		Black purple <i>PPbb</i>	×	Brown <i>ppBB</i>		
		↓		Red purple <i>PpBb</i>		
Male gametes		<i>PB</i>	<i>Pb</i>	<i>pB</i>	<i>pb</i>	F_1
Female gametes	<i>PB</i>	<i>PPBB</i> Red purple	<i>PPBb</i> Red purple	<i>PpB</i> Red purple	<i>PpBb</i> Red purple	F_2
	<i>Pb</i>	<i>PPBb</i> Red purple	<i>PPbb</i> Black purple	<i>PpBb</i> Red purple	<i>Ppbb</i> Black purple	
	<i>pB</i>	<i>PpBB</i> Red purple	<i>PpBb</i> Red purple	<i>ppBB</i> Brown	<i>ppBb</i> Brown	
	<i>pb</i>	<i>PpBb</i> Red purple	<i>Ppbb</i> Black purple	<i>ppBb</i> Brown	<i>ppbb</i> Brown	

The ratio is $\frac{9}{16}$ (red purple) : $\frac{3}{16}$ (black purple) : $\frac{4}{16}$ (brown)

8.7 Inhibitory Factor (13 : 3) : An inhibitory factor is one which in dominant form suppresses or inhibits the expression of the other dominant, but itself has no phenotypic effect. The best example of inhibitory factor is the inheritance of leaf colour in rice. In rice, the purple pigment (P) in leaf is dominant over green (p). There is another factor (I) which inhibits the expression of P and so the leaves become green. It has no effect in the recessive form (i), so in that case the leaf colour will be purple or green depending on whether P is present or not.

When a cross is made between a purple leaf ($PPii$) and green leaf ($ppII$) varieties of rice, all F_1 rice plants, bear green leaf. In the cross between two F_1 plants, 13 (green) : 3 (purple) plants were obtained in the F_2 generation. The cross is given below :

		Purple $PPii$	×	Green $ppII$		
		↓		Green $PpIi$		
						F_1
		Male gametes	PI	Pi	pI	pi
Female gametes	PI	$PPII$ Green	$PPIi$ Green	$PpII$ Green	$Ppli$ Green	F_2
	Pi	$PPIi$ Green	$PPii$ Purple	$PpIi$ Green	$Ppii$ Purple	
	pI	$PpII$ Green	$PpIi$ Green	$ppII$ Green	$ppIi$ Green	
	pi	$Ppli$ Green	$Ppii$ Purple	$ppIi$ Green	$ppii$ Green	

The ratio is $\frac{13}{16}$ (green) : $\frac{3}{16}$ (purple)

8.8 Duplicating Factor or Multiple Factor (15 : 1) : When two pairs of factors situated in different chromosomes affect the same characters and the individual's effect being same, their intraction produces the same quality with intense magnitude it is known as duplicating factor or multiple factor.

A number of genes sometimes affect a character and in which each gene has some small effect. The net result obtained due to the effect of more genes is greater. Such genes are termed as **polygenes**.

A classical example of duplicating factor was first reported by Shull in the capsule shape of shepherd's purse (*Capsella* sp.), in the

inheritance of endosperm colour in maize and kernel colour of wheat. In the inheritance of endosperm colour in maize, when a pure yellow is crossed with white variety, all the F_1 plants are with yellow endosperm. In the F_2 generation 15 (yellow) : 1 (white) ratio was obtained. Since the white variety is about one-sixteenth of the F_2 population, this ratio is of a dihybrid cross and not of a monohybrid cross. Yellow endosperm is due to two independent genes C_1 and C_2 . The presence of either or both genes causes yellow endosperm ; while in the absence of the two, white endosperm is produced. When a yellow homozygous parent ($C_1C_1C_2C_2$) is crossed with a white parent ($c_1c_1c_2c_2$), the F_1 plants have yellow endosperm and the F_2 produces 15 (yellow) : 1 (white) ratio.

		Yellow $C_1C_1C_2C_2$	×	White $c_1c_1c_2c_2$		
		↓		Yellow $C_1c_1C_2c_2$	F_1	
Male gametes		C_1C_2	C_1c_2	c_1C_2	c_1c_2	
Female gametes	C_1C_2	$C_1C_1C_2C_2$ Yellow	$C_1C_1c_2c_2$ Yellow	$C_1c_1C_2C_2$ Yellow	$C_1c_1c_2c_2$ Yellow	F_2
	C_1c_2	$C_1C_1C_2c_2$ Yellow	$C_1C_1c_2c_2$ Yellow	$C_1c_1C_2c_2$ Yellow	$C_1c_1c_2c_2$ Yellow	
	c_1C_2	$C_1c_1C_2C_2$ Yellow	$C_1c_1C_2c_2$ Yellow	$c_1C_1C_2C_2$ Yellow	$c_1C_1c_2c_2$ Yellow	
	c_1c_2	$C_1c_1c_2c_2$ Yellow	$C_1c_1c_2c_2$ Yellow	$c_1C_1c_2c_2$ Yellow	$c_1c_1c_2c_2$ White	

The ratio is $\frac{15}{16}$ (yellow) : $\frac{1}{16}$ (white)

The inheritance of awned-awnless grain in rice and the chlorophyll inheritance in ragi are other example of duplicating factors.

8.9 Polymerisms (9 : 6 : 1) : This is like that of duplicating factor in that when any one of the factors is present (C_1 or C_2), the phenotypic effect is same, but it differs from duplicating factor in that when both of them are present together (C_1 and C_2) at least in a single dose the phenotypic effect is intensified.

The inheritance of pericarp colour in wheat is a typical example of polymerism. Here the two genes C_1 and C_2 are responsible for red colour of the grain. In the presence of both of these genes grain colour is deep red while the presence of any one of them causes light

red colouration of the grain. In the recessive form, however, the grain colour is white.

A deep red ($C_1C_1C_2C_2$) and a white ($c_1c_1c_2c_2$) variety when crossed, produce all deep red plants in F_1 generation. When the F_1 plants are crossed with each other they give 9 (deep red) : 6 (light red) : 1 (white) ratio in the F_2 generation. The mode of inheritance is given below :

		Deep red $C_1C_1C_2C_2$		\times	White $c_1c_1c_2c_2$			
		\downarrow		Deep red $C_1c_1C_2c_2$				F_1
Male gametes		C_1C_2	C_1c_2	c_1C_2	c_1c_2			
Female gametes	C_1C_2	$C_1C_1C_2C_2$ Deep red	$C_1C_1c_2c_2$ Deep red	$C_1c_1C_2C_2$ Deep red	$C_1c_1c_2c_2$ Deep red			
	C_1c_2	$C_1C_1C_2c_2$ Deep red	$C_1C_1c_2c_2$ Light red	$C_1c_1C_2c_2$ Deep red	$C_1c_1c_2c_2$ Light red			
	c_1C_2	$C_1c_1C_2C_2$ Deep red	$C_1c_1c_2c_2$ Deep red	$c_1c_1C_2C_2$ Light red	$c_1c_1c_2c_2$ Light red			
	c_1c_2	$C_1c_1C_2c_2$ Deep red	$C_1c_1c_2c_2$ Light red	$c_1c_1C_2c_2$ Light red	$c_1c_1c_2c_2$ White			

The ratio is $\frac{9}{16}$ (deep red) : $\frac{6}{16}$ (light red) : $\frac{1}{16}$ (white)

Linkage and Crossing over

9.1 LINKAGE : In the previous discussion on dihybrids, two pairs of genes are generally considered to be located on different chromosome pairs. Genes carried in different chromosomes undergo independent assortment and so they produce the ratios of differentiating characters according to the Mendelian expectations. But if the genes are present in the same chromosome they may not follow the same independent assortment which characterised genes located on different pairs of chromosomes but rather they would be linked together in heredity by virtue of their common chromosome. Thus all the genes on one chromosome which tends to move *en block* during meiosis when the chromosomes are segregated into haploid groups are said to be linked genes. This phenomenon is termed as linkage.

Mendel was not aware of this type of happening. Had he observed it, he would have to modify his principle of independent assortment, for linked genes are not assorted independently.

The existence of linkage was predicted by Sutton (1903) before it was actually discovered. Sutton observed that since the number of hereditary units is much larger than the number of pairs of chromosome, then each chromosome pair must contain a number of pairs of genes and since the chromosomes move as units during meiosis, all the genes of one chromosome will be linked together. Three years later in 1906 Bateson and Punnett first demonstrated the phenomenon of linkage in sweet pea. They observed a departure from the Mendelian ratio when they crossed plants of different flower colour and pollen shape. They found that the genes for flower colour and pollen shape did not completely assort independently but were tied together, so that the F_2 ratio contained too many of the parental combination and too few of the recombination. Although Bateson and Punnett discovered the phenomenon of linkage, they did not succeed in giving any correct explanation of this interesting deviation from Mendelian segregation. It was Morgan who in 1910 in his investigation with the fruit fly, *Drosophila melanogaster* advanced the basic idea that the degree of linkage depends upon the distance between the linked genes in the chromosome. This idea has established that genes have a linear arrangement in the chromosome and are located in a constant and definite order and they occupy the same locus in the chromosome.

Soon after the linkage and crossing over was established in *Drosophila*, this phenomenon has been found to occur in other plants and animals. The first clearly recognized linkage in maize (*Zea mays*) was reported by Collins and Kempton (1911). They observed that the gene for waxy endosperm (*WX*) was linked with the gene for

aleurone colour (*C*). The principle of linkage was thus firmly established in plants and animals.

In some cases, the genes in the same member of a pair of chromosomes would always stay together and thus make linkage *complete*. The male fruit fly (*Drosophila*) and the female silk moth (*Bombyx*) ordinarily have no crossing over, that is they have *complete linkage*. There are cases like tomato and wheat, where some percent of crossing over always takes place, even though the genes are linked. This type of linkage is known as *incomplete linkage*.

Detection of linkage : Backcross or test cross¹ is the most convenient way to determine linkage within genes and the relative position of the genes within the chromosome.

When the F_1 plant for two pairs of genes on different chromosomes is crossed with a fully recessive individual, a ratio of 1 : 1 : 1 : 1 is expected. This ratio (1 : 1 : 1 : 1) clearly indicates the independent assortment and a significant departure from this ratio among the F_2 offsprings can be confidently ascribed to linkage.

Maize is the most thoroughly studied plant where linkage has been detected. Hutchison crossed a variety of maize having seeds coloured and normally filled out (full) with a colourless and shrunken seeds. Here in this experiment coloured (*C*) is dominant over colourless (*c*) and normal or full endosperm (*S*) is dominant over shrunken (*s*). The parents are therefore coloured full (*CCSS*) and colourless shrunken (*ccss*), which however give a coloured full phenotypic plant in the F_1 generation with the genotype *CS/cs*.

Now if *C* and *S* assort independently in the backcross of such experiment, these F_1 plants should produce four types of gametes (*CS*, *Cs*, *cS* and *cs*) in equal number according to Mendel's second principle. But in the actual cross however, this expectation was not realized. The coloured full and colourless shrunken (*parental combinations*²) are more frequent than the coloured shrunken and colourless full (*recombinations*²). In independent assortment, the parental combinations (*CS* and *cs*) and recombinations (*Cs* and *cS*) would be equally frequent. But the actual data indicate the parental combinations are about 96.4% whereas the recombination are about 3.6% of the total.

So, it is obvious from the above experiment that the genes *C-c* and *S-s* have not assorted independently. Here the parental combination exceeds the expected 50%, rather they linked or combined in 96.4% and are recombined in only 3.6%.

¹ A cross of a hybrid with one of its parents is known as **backcross**. Test cross however signifies to those backcross where the cross with the recessive parental type is involved. It is used to test whether the individual is homozygous or heterozygous. If homozygous, all offsprings show dominant phenotype; if heterozygous, half show dominant and half recessive phenotypes. It also used to test the linkage.

² Some geneticists have used the term "coupling" for the double dominant and double recessive (*CS* and *cs*) combinations and "repulsion" for the mixed dominant-recessive (*Cs* and *cS*) combinations.

If, however, another experiment was done with the same genes in different association i. e. if plants with colourless full seeds were crossed with those of coloured shrunken seed, the parental combination here again is in excess (97.06%) more than the recombination (2.94%) although the parental combinations are just the opposite of

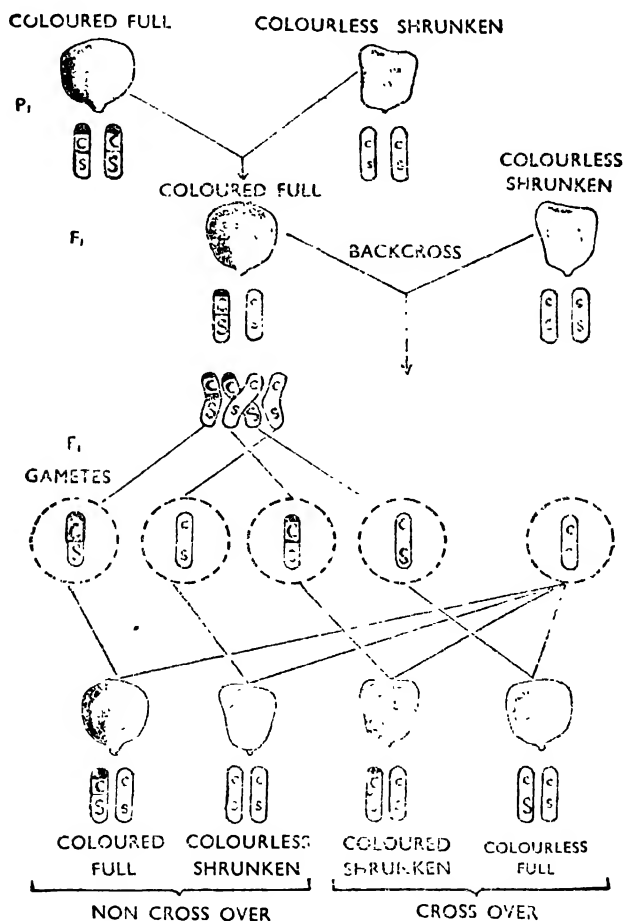


Fig. 9.1 Diagram showing linkage and crossing over in corn.
Non-crossovers=96.4% and cross overs=3.6%

what they were in first experiment. It can conclusively be proved therefore that whatever may be the parental combination of two different pairs of linked genes, linkage tends to keep them together and thus the cause of departure of a 1:1:1:1 ratio among the F₂ offsprings is definitely due to linkage.

Importance of linkage : A knowledge of linkage is essential, before any programme of hybridization is taken up. If any desired character is linked with any undesired character, the attempt to incorporate the desired ones is likely to meet with failure. Such hybridization is only possible after mutating the undesired character.

When any qualitative character is linked with any quantitative character an expression of quantitative character will reveal the presence of the other. For example, anthocyanin pigmentation in rice is linked with high yield. So, any plant with anthocyanin pigmentation will reveal its high yielding quality.

Sometimes, qualitative characters, such as, leaf shape, stem colour etc. are linked with quantitative character, such as size of fruit, weight of seeds etc.

When plants are crossed, the occurrence of the easily recognisable qualitative character in the progeny can serve as an index of the linked quantitative character for selection purpose, because the entire group of linked genes will be inherited as a block, except, of course, when the linkage is broken by crossing over. Such genes are called **marker genes**. Thus in rice, anthocyanin pigment serves as a marker for yield and grain colour for weight of grain. Sometime in cotton, the lint colour serves as a marker for lint length.

9.2 CROSSING OVER : During diplotene of the prophase-I of meiotic cell division exchange of chromosomal segments occurs and

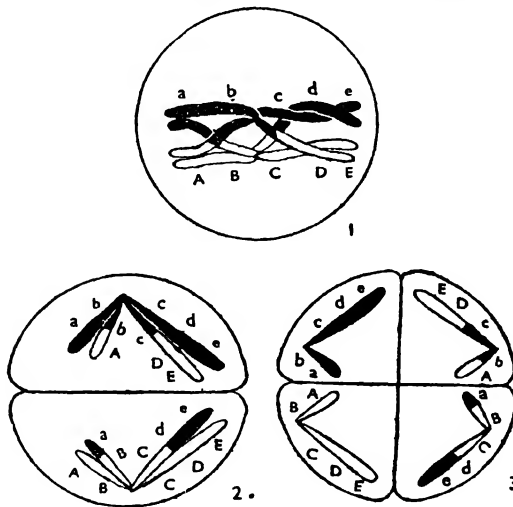


Fig. 9.2 1. Diagram showing chiasma formation and crossing over [paternal (black) and maternal (white) homologue]. 2. The two chromatids are genotypically different at the anaphase stage. 3. Shows four daughter cells due to separation of chromatids (2 parental and 2 recombinant)

according to Morgan this interchange of chromosomal material from one chromosome to another chromosome is termed as **crossing over**. In this mechanism, a group of genes changes their place with a similar group of genes between two homologous chromosomes. Here interchange of maternal and paternal chromosomes occurs giving rise to new gene combinations. In the prophase-I of meiosis, pairing between two homologous chromosomes occurs. Next the paired chromosomes become double, each of which forming two chromatids. The chromatids slightly separate from each other and a visible distinct cross is formed called **chiasma**, which represents the regions where crossing over occurs. The behaviour of the chromosomes can be represented in the Fig. 9.2.

Cytological basis of Crossing over : Although the genetic evidence for crossing over became well established by Morgan (1914) and his associates ; this however, can not be demonstrated cytologically because the homologous chromosomes are microscopically alike. The actual exchange of chromosome blocks is therefore very difficult to observe unless some markers could be incorporated on the chromosomes. So the correctness of the genetical evidence can be proved only by the use of heteromorphic pair of chromosomes. The work of Stern (1931) in *Drosophila melanogaster* and Creighton and McClintock (1931) with maize provides good support of this long awaited problem.

Stern (1931) in his experiment observed a strain of *Drosophila* in which a portion of the Y-chromosome had become broken off and through translocation attached to the X-chromosome. Thus this X-chromosome forms a L-shaped body, easily recognizable under the microscope. Thus the female strain can be obtained one of whose X-chromosomes is normal rod like structure and the other X-chromosome is typically L-shaped. In another strain, a part of the X-chromosome had been broken off by X-ray treatment and the broken part became attached to the small 4th chromosome in *Drosophila*. Thus the two X-chromosomes were therefore recognizable under the microscope.

In addition, one of the X-chromosomes carried the mutant alleles for carnation (Cr) and bar (B). Carnation is the recessive light eye colour whereas the bar is the semidominant narrow eye shape. A female can be raised from such a cross whose one of the X-chromosomes is with the translocated part from Y-chromosome and carries the normal alleles of carnation (+cr) and bar (+B). The other X, however, has been broken into two separate parts, the parts bearing centromere carries the gene Cr and B.

When such a fly with a genotype (Cr B/+cr+B) is crossed with a male having both the recessive genes (Cr+B) i.e. carnation non-bar, the female non-crossover offspring of the mating should be phenotypically carnation-bar (Cr B/Cr+B) and wild type i.e. non-carnation and non-bar (+cr+B/Cr+B). On cytological examination of the female flies, the former bears two X-chromosome fragments while the latter bears one X-chromosome bearing the piece

of the Y-chromosome. Both however, possess one X-chromosome coming from the male parent. Genetic crossing over will produce females of different phenotypes, carnation non-bar ($Cr+B/Cr+B$) and non-carnation and bar ($+cr B/Cr+B$). On cytological examina-

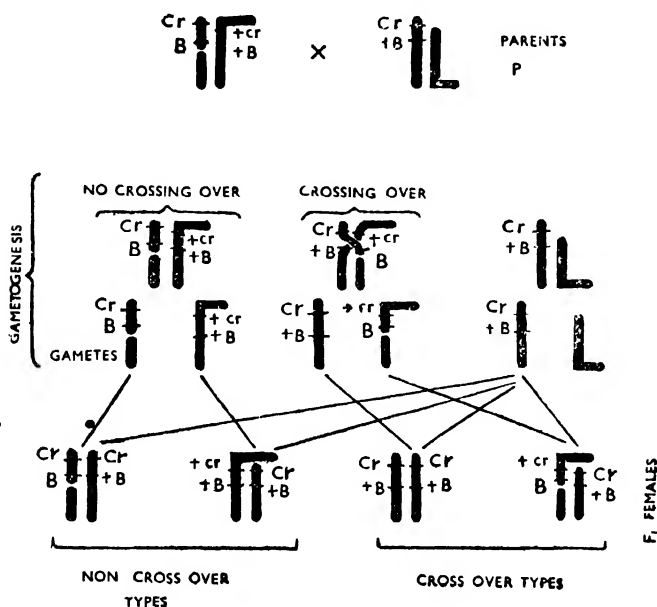


Fig. 9.3 Diagram showing crossing over between female *Drosophila* carrying abnormal chromosome and carnation males. The two X-chromosomes in the females are distinguishable. Bar (B) = narrow eyes. Carnation (Cr) = an eye colour

tion, again the former contains two X-chromosomes, one of which is a long X-chromosome while the latter contains one X-chromosome with attached Y-portion. Here also both of them possess one X-chromosome coming from the male parent. The genetic and cytological results are given in Fig. 9.3. Of 364 such F_1 female flies, with the exception of only 5, Stern observed a complete correspondence between genetical and cytological facts. So the genetic crossing over is accompanied by the cytological exchange of chromatic materials.

In maize, Creighton and McClintock (1931) carried out experiments almost similar to those of Stern with *Drosophila*. Their experiments are based on the heteromorphic pair of X-chromosomes, one X with satellite chromosome and the other is very short through deletion. One of the female X-chromosomes in with coloured-starch character gene and the short X has white-waxy character gene. Such female is now crossed with a male whose X-chromosome carries white-waxy gene. The genetic and cytological study of the above cross clearly indicate the correlation between them.

Mechanism of Crossing over: The mechanism by which the recombination of genes or crossing over takes place is a matter of large controversy. Three different theories have been proposed to account for crossing over.

The classical theory has been proposed by Sax (1932) which may often be referred to as the "*two plane theory*" of crossing over. According to this hypothesis the duplication of chromatids must have occurred prior to synapsis. The paired homologues remain relationally coiled in the early part of the meiotic prophase pachytene. The coiled homologues then open in diplotene. As

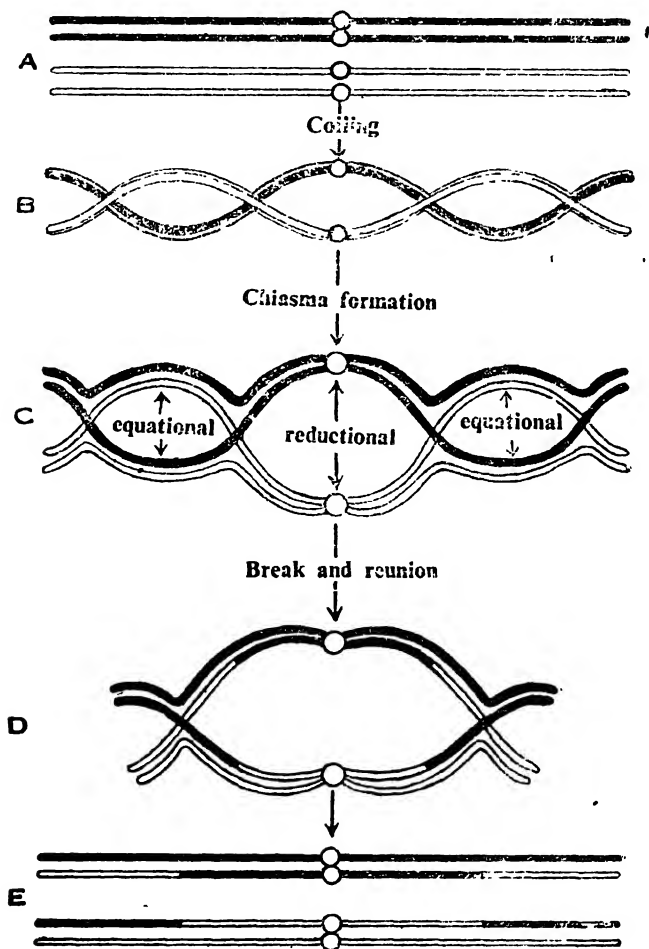


Fig. 9.4 Diagram showing the possible interpretation of crossing over according to classical theory of Sax (1932)

a result of this, the centric loop shows a pair of sister chromatids and the adjacent loops contain paired non-sister chromatids. Due to further contraction of the chromosomes, the loops bow out further and a stress is imposed at the point of chiasma which ruptures the two chromatids. The broken chromatids then rejoin and thus the loss of chiasma and the induction of crossing over takes place (Fig. 9.4).

Another interpretation is the chiasmotypy hypothesis proposed by Janssens (1909, '24) and later on elaborated by Darlington (1934, '35, '37). According to this theory crossing over occurs in the early

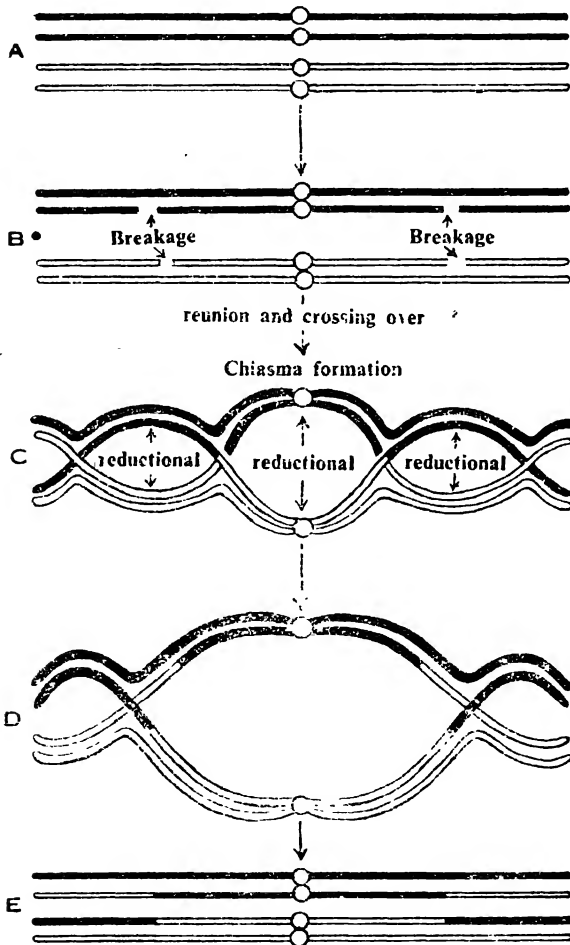


Fig. 9.5 Diagram showing the possible interpretation of crossing over according to chiasmotypy hypothesis of Darlington (1934-37)

meiotic stage. This is, however, correlated with the pachytene when the homologous chromatids are closely paired. Towards the onset of metaphase, a chiasma is formed at the point where crossing over has occurred. So according to this conception, a chiasma always represents a genetic crossover i.e. the exchange of genetic material leads to the formation of a chiasma (Fig. 9.5).

Some of the problems of the pairing mechanism, which like the pairing of three sets of homologous chromosomes (triploids) are inexplicable by the classical theory, have however been explained by Darlington (1934) in the chiasmotypy theory. It has been observed that the pairing of the chromosomes will take place with one of their homologues at a time, no matter how many homologues are carried by the organism. Further support to this theory came from the correlation between the number of chiasmata and cross over (Beadle, 1932 ; Brown and Zohary, 1955).

But the most serious objection to chiasmotypy hypothesis has been provided by Kaufmann (1934) and Cooper (1949). They observed the chiasmata in some tissues of male *Drosophila* where genetic crossing over is absent. Slizynski (1964) however interpretes this chiasmata in male *Drosophila* as a surface association rather than cytological exchange.

A somewhat different theory of chromosomal crossing over was proposed by Belling (1931, 1933). According to him break and reunion is not the cause for crossing over but rather recombination results from a novel arrangement which occurs when new strands are formed. Belling considered that the new genes were formed first alongside their respective genes and the interconnecting fibers formed later. If the homologous chromosomes are relationally coiled, the inter connecting fibers will join to their closest neighbours and thus the new genes will show cross over. Although the experimental and observational data are quite lacking in explaining this theory in higher organisms, but this theory fits with the "copy choice" method developed to explain the duplication process in virus. So this theory is most attractive to the physiological geneticists and can often be referred to as copy choice theory (Fig. 9.6).

According to this theory the two original strands remain intact and the crossing over occurs between the two newly formed strands, so, two of the four chromatids are involved in crossing over. But the data on *Neurospora* and *Drosophila* clearly indicate that the crossing over occurs at the four-strand stage. Another problem of this theory is the time of duplication of strands which however, according to this theory occurs in meiosis, but the evidence indicates that in higher organisms, DNA replication occurs before the pairing process in meiosis.

So, considering all the problems regarding crossing over it can be safely stated that there must exist more than one mechanism to account for crossing over. Of all the theories the present weight of evidence, however, would favour the break and joining explanation.

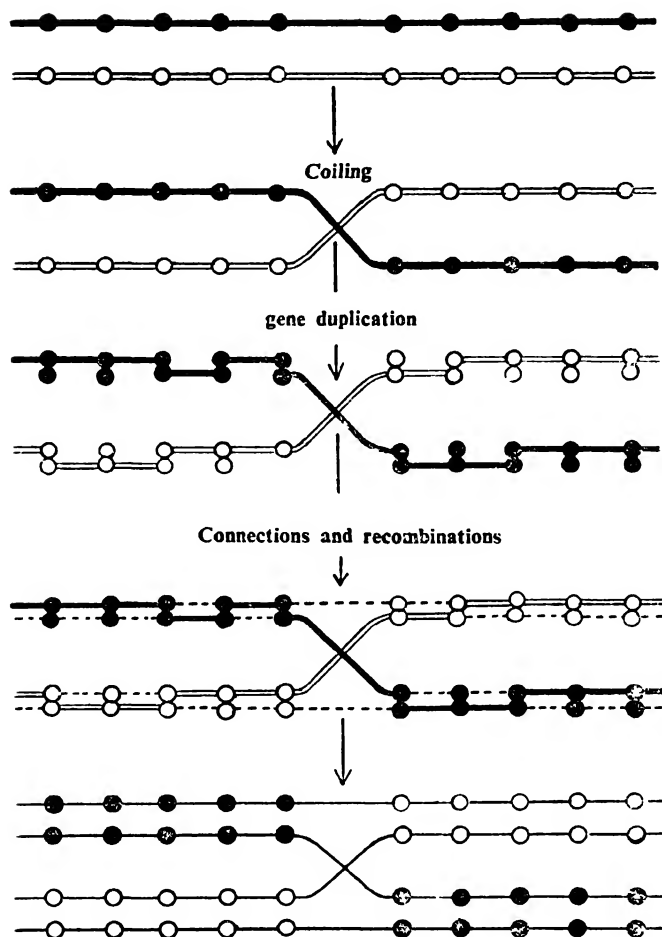


Fig. 9 6 Proposed interpretation of crossing over according to Belling (1933)

Significance of Crossing over : With the exception of few organisms, crossing over is a widespread phenomenon in all higher plants and animals, as well as in yeasts and molds, viruses and bacteria. It is of utmost significance in the development of sexual reproduction in plants and animals. Crossing over helps in the great genetic diversity by reorganization of the genetic complement. Thus it helps indirectly in the increased evolutionary potential in the organisms.

That the genes are arranged in a linear fashion and occurrence of organized linkage groups can be proved by experimentally utilizing this method. All these facts laid the foundation for analyzing the genetic mechanism and investigating the nature of the gene.

It is evident from the Mendelian principles that the hereditary trait is carried through the genes in the chromosomes. Till the work of Muller (in the early part of present century) the genes were considered to be quite stable and unchangeable. Muller (1927) first observed that genes can be changed and so are quite different from the original form. This change will therefore, definitely, affect the genetic make up in the organism which will be expressed as a modification of form and function. This genetic change is therefore capable of altering the phenotype of the individual and pass from one generation to the next. *This permanent change in the phenotype of the organism due to change in the hereditary material is termed as mutation.* Although mutation may occur spontaneously in nature due to some metabolic conditions within the body of the organisms, but such gene changes may also be incorporated by the application of radiations, chemicals and other means.

Mutations are of two distinct types. In one case there is either a physical or chemical change in the gene at the molecular level. This is known as **gene or point mutation** or **intragenic change**. In another case the change in the organism may be due to the gross morphological change in the structure of the chromosome. Such a gross change in the chromosome is termed as **chromosomal aberration** or **chromosomal mutation**. Since this change always takes place within a chromosome, it involves two gene loci. It is often therefore termed as **intergenic mutation**.

In recent years the term 'mutation' is used in a more restricted sense where the process of direct alteration of gene contents is involved. So in this sense gene or point mutation is the true type of mutation and so the gene mutations are considered only in this chapter. Chromosomal mutation may be due to change in the number of the whole genome (for detail refer chapter 5) or in the structure of the individual chromosome (for detail refer chapter 4).

When a change of structure or chemical composition occurs within an individual gene, it is called an intragenic change. Genes are the bodies situated on the chromosome which are responsible for the development of hereditary characters. Genes are generally stable bodies but sometimes undergo minor changes. The gene which undergoes changes is called a *mutated gene* and the phenomenon is called **gene mutation**. The gene mutation occurs at a particular fixed point of the chromosome hence it is also called **point mutation**. A mutated gene in some cases can again undergo mutation to form the original gene, called *reverse mutation*. Gene mutation is spontaneous and is a very natural phenomenon.

It has been established from the recent findings that deoxyribose nucleic acid (DNA) is the main chemical constituent of a gene. Since DNA can be changed, its influence on the organism can also be changed and so some phenotypic alteration must be associated with the gene change. The smallest part of DNA which is effective in causing a mutation is known as **muton**. This change in the chemical nature may be presumably minor without producing any phenotypic alterations. Whereas in major cases the change is very much pronounced and sudden. Such alterations are heritable and therefore influence natural selection and thus represent a factor in evolution.

Since majority of the mutations are recessive, all mutations are not immediately detectable. They only can express themselves in a homozygous form.

Mutation can occur either in the autosomes or in X-chromosomes. When it occurs in X-chromosomes, it is sex-linked.

Various mutations are observed in *Drosophila melanogaster*, which give rise to stable true-breeding genotypes. They vary from the original wild species by some characters like wing type, eye colour etc. Mutations in some cases cause disastrous effects on the individual, when the mutation is called *lethal*.

In the developing organisms mutation may occur in any cell at any stage in the cell cycle. If a mutation occurs in the somatic cell of the organism, it immediately reproduces other cells like itself but not the whole organism. When the new individual develops from such cells, it is said to be **somatic mutation**. Many of the delicious apple and orange varieties are example of typical somatic mutation. When, however, mutation occurs in the germ cells it can reproduce entirely a new organism and the type of mutation is known as **germinal mutation**. Like somatic mutation germinal mutation also occurs, at any stage of cell cycle, but they are more common during the gene duplicating process. Germinal mutation occurs in all plants and animals. When out of the two homologous chromosomes in the fertilized egg, one undergoes mutation, they will produce an individual where half of the body is mutated and the other half is normal. In this case if the mutation is predominant the individual is called **mosaic** or **fractional mutant**.

Induced Mutations : Artificially, mutations can be induced by means of X-rays. Muller (1927) first observed in *Drosophila* that by applying X-rays, mutation rate can be increased. This effect has been supported later on by a number of workers and it has been suggested that the effect of irradiation was destructive due to loss of some substances from the chromosome or total destruction of the gene. Other rays like ultraviolet can also induce mutation, although not much pronounced like X-rays. Many chemicals like mustard gas, colchicine, sulphanilamide, benzene, formaldehyde, β -propio lactone, phenyl acetic acid, phenol etc. can also induce mutation. The chemicals or rays should be applied very carefully in definite dose,

otherwise heavy dose will cause serious disease whereby degeneration will occur and finally lead to the death of the organism.

Besides these physical and chemical mutagens, some environmental agents like temperature are able to cause somatic mutation. Germinal mutations, however, can not be induced by any environmental factor.

Basis of Mutations: The radiations that are important in mutation may be *ionizing radiation* includes X-rays, gamma rays, alpha and beta rays etc. or *non-ionizing radiation* includes ultraviolet (UV). Relatively little is known about the mechanism by which ionizing radiation produce mutations. One of the known effects of ionizing radiation is the breakage of chromosomes and chromatids. Such break involve in the sugar-phosphate backbone of the polynucleotide strands. Two simultaneous breaks in the same chromosomes can lead to deletion or inversion while simultaneous breaks in non-homologous chromosomes can lead to translocation (for details refer Chapter 4). X-ray induced chromosomal aberrations are more frequent at high O_2 tensions. X-ray actually act in an indirect way. O_2 produce H_2O_2 and H_2O in irradiated water and it may be these products that induce the break. When ultraviolet (UV) light is absorbed by nucleic acid, the absorbed energy can cause alterations in the bond characteristics of the purines and pyrimidines. Such type of base alteration is known as *photoproducts*. Pyrimidines are more liable to such changes than purines.

In some cases there is a rearrangement in the distribution of hydrogen atoms in the four bases of DNA (when it is called rare state). These rearrangement are called *tautomeric shifts*. When the base is in the rare state it cannot be linked to its normal partner. Thus if adenine is in a rare state during DNA replication, cytosine can pair with it. This situation is very unstable and in the next replication adenine after returning to its common state pair with thymine. Cytosine introduced into the complementary strand due to tautomeric shift in adenine would pair with guanine. Such change in the nucleotide chain is called *transition*.

Detection of Mutations: Although Muller induced mutation in *Drosophila* in 1927 by the application of X-rays, actually attempts were made many years before 1927 to test this possibility. It took nearly about ten years for Muller (1920) to find out a suitable technique viz. the classical *CIB* method for detecting sex-linked lethals.

In *Drosophila melanogaster*, the *CIB* fly carries an inversion (C) in the X-chromosome, it acts as a crossover suppressor, a recessive lethal (*l*, no expression in heterozygous female) and a dominant gene bar (*B*, narrow eyes). The *CIB* females are bar-eyed, whereas the male getting this chromosome dies on account of lethal gene. A cross between a *CIB* female (identified by bar-shaped eye) with a normal male gives a sex-ratio 2 (females) : 1 (male). Half the male progeny possessing the sex-linked lethals will die. The purpose of

this cross is to obtain a female whose sources of her two X-chromosomes are known and identifiable.

To carry out *CIB* test, males which have been X-rayed are mated with *CIB* females. Here also the ratio is 2 (female) : 1 (male). The

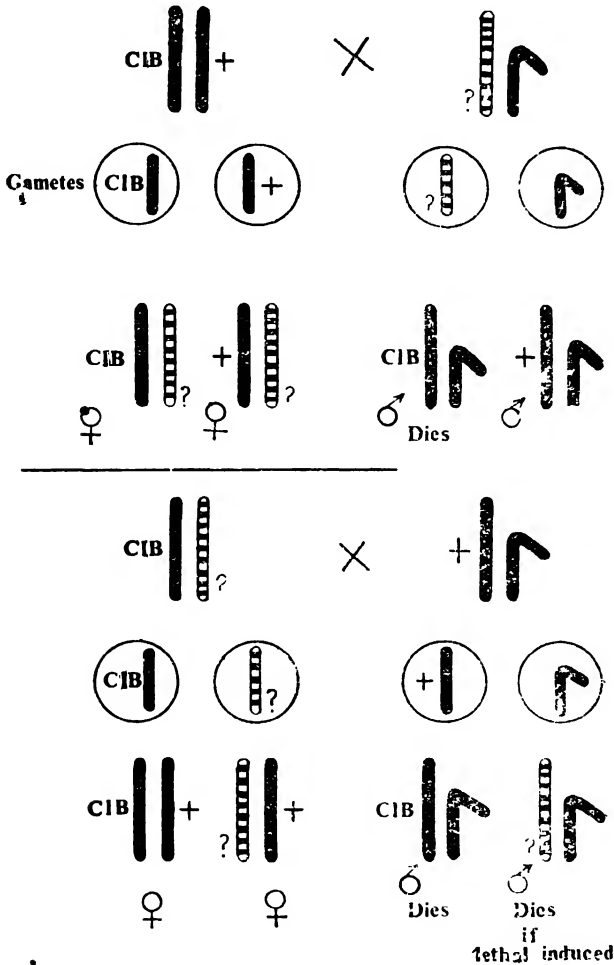


Fig. 10.1 *CIB* method for the detection of gene mutation in *Drosophila melanogaster*

F_1 bar-eyed females receive one *CIB* X-chromosome from the mother and the another X-chromosome receive from the male which has been X-rayed. But the females would not die as the genes are non-allelic. In a cross between such F_1 bar-eyed female with a normal male half of the males die because of the lethal gene in the *CIB* chromosome and the other half will also die because of the newly

arisen lethal in the other X-chromosome. As a result of such a cross, therefore, no males and only the females will survive. Thus the fact that no males are formed in the above cross is sufficient to identify the occurrence of a lethal sex-linked recessive mutation in *Drosophila* (Fig. 10.1).

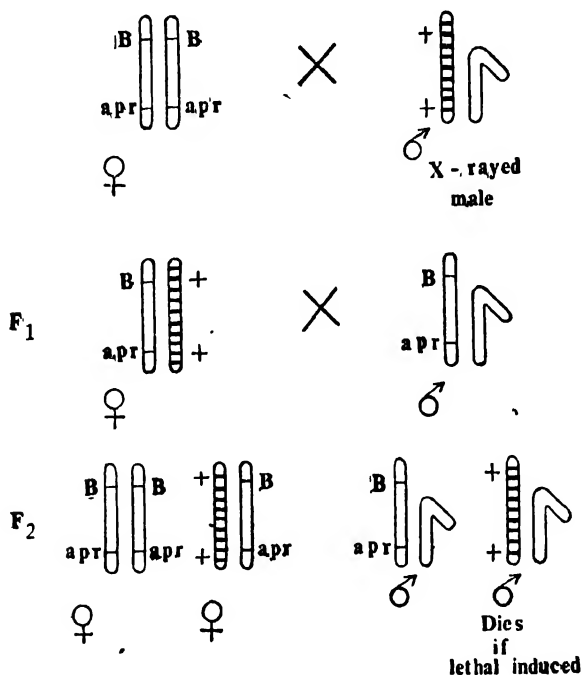


Fig. 10.2 *Muller-5* method for the detection of gene mutation

A modern version of Muller's technique is known as *Muller-5* or *Base*. Muller-5 stock carries a complex inversion system and consequently has a better cross over suppression. It does not carry any lethal gene but in addition contains two marker genes, one for eye colour (*apricot*) and another for eye shape (*bar*). When a cross is made between such Muller-5 females and wild type males, it produces F₁ females in which crossing over in the X-chromosome does not occur. In the F₂ progeny two kinds of males and two kinds of females are produced. In the males one is Muller-5 and the other is wild type whose one of the X-chromosomes is transmitted by the grand parent. If this wild type male (grand parent) carries a lethal in its X-chromosome (by irradiation), no wild type males will be produced in the F₂ generation. Thus the mutation can be tested (Fig. 10.2).

CHAPTER 11

Sex Chromosome and Sex Linkage

11.1 Sex Chromosomes : Sex is determined as soon as the egg is fertilized by sperm and that it depends on the gametes. Sex, like all other characteristics of the living organism, has a genic basis. The first investigation relating chromosome to sex came from the work of a German biologist Henking in 1891. He showed a particular nuclear structure during spermatogenesis in certain insects. This structure is present in half of the sperms, whereas the other half did not receive it. Henking however, was unable to give any explanation why this was present in some sperms and absent in others ; but he designated this structure as 'X'. In 1902 association between the sex characteristics and the presence and absence of this particular structure was put forth in definite form by McClung. McClung who made cytological observations on male grasshoppers demonstrated that this X body is associated with sex determination. He however, was unable to show the presence of this accessory or sex chromosome in females and so concluded that only the male contained the sex chromosome. Finally, in 1905 Wilson and Stevens however showed that both male and female carry this chromosome. *These chromosomes which are different in their visible morphology and in their influence upon sex, are termed as sex chromosomes.* The rest of the normal chromosomes in the body are termed as autosomes.

These sex chromosomes are usually designated as X and Y. The majority of the diploid sexual organisms have a pair of this sex chromosomes. Usually the females have two similar chromosomes.

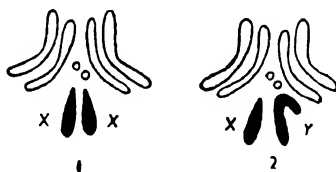


Fig. 11.1 Sex chromosomes in *Drosophila melanogaster*
1. Female, 2. Male

(XX) while the males usually possess one X and one Y (XY). This XX females and XY males is characteristic of mammals including man and in certain insects such as *Drosophila* (Fig. 11. 1). Here the female produces only one type of egg whereas the male produces two types of sperms. So the female producing gametes of one type is termed the homogametic sex. Whereas the male forming two types

of gametes, with or without the X-chromosome is termed as the heterogametic sex.

In some vertebrates (birds, some reptiles and fishes) and invertebrates (like insects of the order Lepidoptera) the females are heterogametic and males are homogametic. In Orthoptera the males are XO and females XX. In the axolotl, however, sex depends on the presence or absence of Y-chromosome.

In some organisms, however a number of X-chromosomes act together as the sex determining factor. Thus in *Ascaris incurva* there is a large difference in the number of chromosomes between males and females. Males have 8 X-chromosomes and one Y in addition to their normal 26 autosomes. So they produce two types of gametes ($8X + A$ and $Y + A$) while the females produce only the former type. The extreme example of compound sex chromosomes occur in beetle (*Blaps polychresta*), where the male has $12X$ and $6Y$ in addition to 18 autosomes. In mammals including man Y-chromosome determines the male sex. Thus an individual lacking Y-chromosome i.e. XO individual, resembles a female but lacks ovaries (Turner's syndrome).

Whatever may be the sex chromosome complement in the living organism the behaviour of the sex chromosomes in meiosis and syngamy takes place normally.

In many organisms the sex chromosomes are quite different in size and shape, Y is smaller than X and even in some cases Y is practically absent. In some cases however, X and Y are very much alike and are not distinguishable under the microscope.

According to Muller and Darlington crossing over between X and Y-chromosomes is restricted only to certain regions. This segment is known as *pairing* or *homologous segment*. Whereas the other part where the sex differentiating genes are situated undergoes no crossing over. This segment is termed as *differential segment* (refer Fig. 11.4 and 11.5). The genes in the differential segment of Y-chromosome, if do not play any important role in sex determination, will become ultimately lost. Such losses of genes from differential segment of Y-chromosome will ultimately make the chromosome inert as it is found in the Y-chromosome of *Drosophila*.

During reduction division X and Y separate, each going to two separate poles. So at the end of second division two haploid gametes, each containing either X or Y-chromosomes are produced. In cases where there is multiple X-chromosome, there also Y is separated out from multiple X group at the end of first meiotic division and gamete formation takes place as for single X-chromosome. Individuals with compound Y-chromosome also act similarly. In XO species, the X-chromosome does not have a pairing mate, so during meiosis X goes to one of the poles with autosomes. So two types of gametes are formed one with X and autosomes and the other with only autosomes with no X-chromosome. Occasionally as in *Protenor* (squash bug) the first meiotic division is equational for the X-chromosome but the method of gamete formation is usual like XO method.

In man, the X and Y-chromosomes are practically larger than *Drosophila* (Fig. 11.4) and chiasmata are formed between them. Here the genes in the X-chromosome will show sex-linked inheritance like those in the X-chromosome of *Drosophila*. If crossing over, however, occurred between X and Y, some genes from X may be transferred to Y and thus some characters may be transmitted from father to son. The frequency of such exceptions will however be based on the frequency of crossing over between X and Y.

11.2 Sex Linkage or Sex-linked Inheritance or Inheritance related to Sex :—Sex chromosomes are not only the determiner of sex in living organisms they also carry some genes which are responsible for the expression of certain non-sexual characteristics of an organism. The inheritance of characters through genes present in the sex chromosomes and often related with sex is termed as **sex-linked inheritance**. Most sex-linked genes are present in the X-chromosome. In some animals, however some genes with visible effect is present in the Y-chromosome. These Y-linked characters are transmitted directly from the male parent to the progeny. Since Y-linkage is rare, sex linkage usually implies X-linkage. Although sex linkage is referred to best in man and animals, evidence for sex linkage has also been found in some plants like date palm and *Melandrium* (Onagraceae).

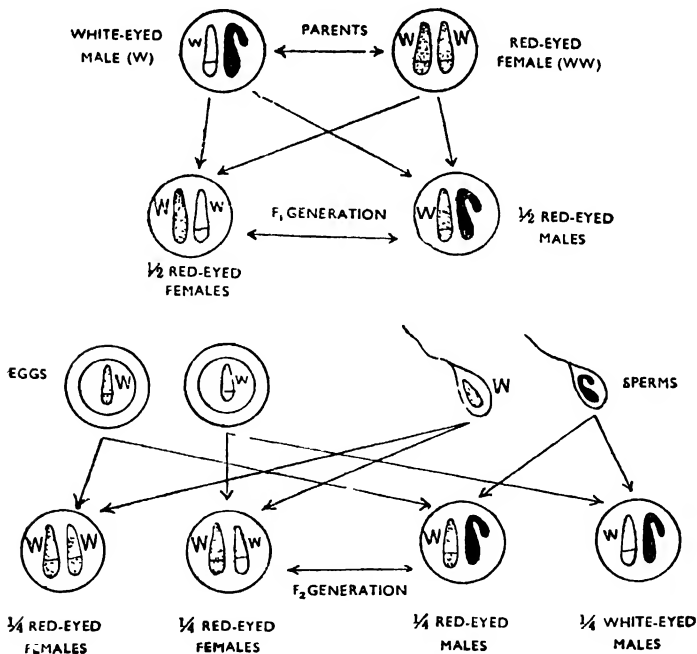


Fig. 11.2 Diagram showing sex linkage in *Drosophila*

The first experimental evidence for sex linkage came with the discovery by Morgan in 1910 of the white-eyed mutant in *Drosophila melanogaster*. According to Morgan a white-eyed male had appeared in a culture of red-eyed flies. The new white-eyed male was mated with a red-eyed female. The F_1 flies were all red-eyed. The F_2 included both red and white in the ratio of 3(red) : 1(white). Further observation showed that all white-eyed flies were males. Of the F_2 males half had white-eyes and half had red and all females had red-eyes i.e. F_2 of such cross did not produce white-eyed females (Fig. 11.2). This experiment indicated that red-eyes were dominant over white and the recessive gene apparently expressed itself only in the males. Such expression according to Morgan can only be explained by considering this gene to be in the X-chromosome.

The male possesses only one X-chromosome and an unlike Y-chromosome. So a single gene for white eyes was capable of expression when its allele was absent. Such males are considered **hemizygous** which have only one member of an allelomorphic pair of genes. In the above cross the gene present in the X-chromosome of the mutated white-eyed male passed on to his daughter. All the females are therefore carrier for the gene. In the F_2 , the males received their X-chromosome from heterozygous mother. Half therefore, received red gene and so half are red-eyed and other half received white gene and therefore, are white-eyed. White-eyed female, however, did appear when F_1 red-eyed females were back crossed with the white-eyed males. In the F_2 of this cross four classes of offspring, white and red-eyed males and females were produced. White-eyed females can only be produced when both the X-chromosomes carry the recessive gene for white.

Thus it is evident that males inherit their X-chromosomes only from their mother whereas females obtain an X-chromosome from each parent. The X-chromosome therefore follows **crisscross inheritance** beginning from P_1 male passing on the F_1 daughter and then to the F_2 sons.

Sex-linked genes, therefore, are expressed more frequently in males than in females and are transmitted from the male through his daughter to his grandsons. Rarely they occur in both father and son.

There are three types of sex-linked inheritance (i) *X-linked* genes located in the non-homologous part of X and hence no corresponding alleles in Y (ii) *Y-linked* genes located in the non-homologous part of Y and have no corresponding alleles in X and (iii) *XY-linked* genes located in the segment that is homologous in both X and Y (so-called incomplete linkage).

X-linked inheritance—The classic example of the linked inheritance is Morgan's eye colour experiment in *Drosophila* which has been thoroughly explained above. The pattern and explanation for sex-linked inheritance in *Drosophila* applies equally to certain inheritance in man. Most important of them are red-green colour

blindness, hemophilia (a defect of blood clotting) and other traits which are associated with X-linked genes in man. The colour blindness is due to a single recessive gene (rg) present in the X-chromosome of male. Similarly in the presence of a single recessive gene (h) in males, clot formation is abnormal and so the disease is hemophilia. X-linkage has now been indicated for more than thirty human traits. Besides the above two important traits, other distinctive traits are : optic atrophy (degeneration of the optic nerve), juvenile glaucoma (hardening of the eyeball), muscular dystrophy (degeneration of certain muscles), defective iris, epidermal

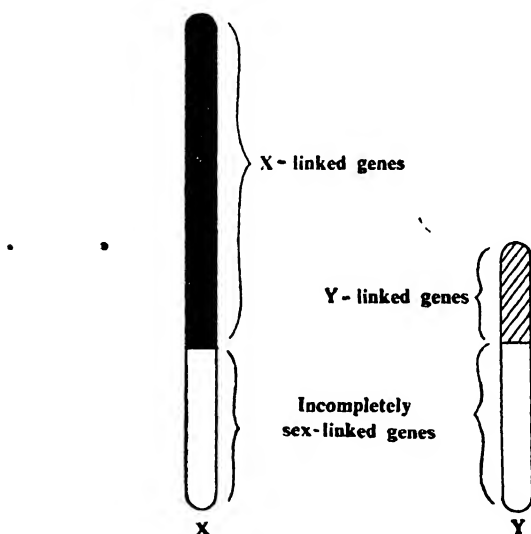


Fig. 11.3 Arrangement of genes in the sex chromosomes in *Drosophila*. Only incompletely sex-linked genes have their alleles on both X and Y-chromosomes

cysts etc. (Fig. 11.4). All these anomalies are transmitted in the same way as the eye colour in *Drosophila* and the same explanation can be given for F_1 and F_2 generations.

Y-linked inheritance—There are few genes present in the non-homologous region of the Y-chromosome of the male (often referred to as “holandric genes”). When the inheritance is related with this particular gene of the Y-chromosome, we call it as Y-linked inheritance. Here the pattern of inheritance is quite different from the X-linked inheritance. Here the genes pass directly from father to son. Although there are some 150 Y-linked genes in *Drosophila* (Fig. 11.3) and few such are known in man, but the pedigrees showing this pattern have not been well substantiated and even the results of some spectacular cases are not accurate. Hypertrichosis (long hair growth

of the ears), ichthyosis hystrix, ichthyosis congenita and other skin diseases are most likely to be Y-linked. But the question of Y-linked inheritance in man should be withheld until substantial evidences are available.

XY-linkage—The genes present in the homologous part of the X- and Y-chromosomes remain as allelic pairs and segregate like ordinary autosomal pairs, although they do not segregate independently of sex as do autosomal genes. Although the genes are present in the X-chromosome, the usual crisscross pattern of sex inheritance is not expected as they remain in a paired (allelic) arrangement. They are therefore said to be incompletely sex-linked.

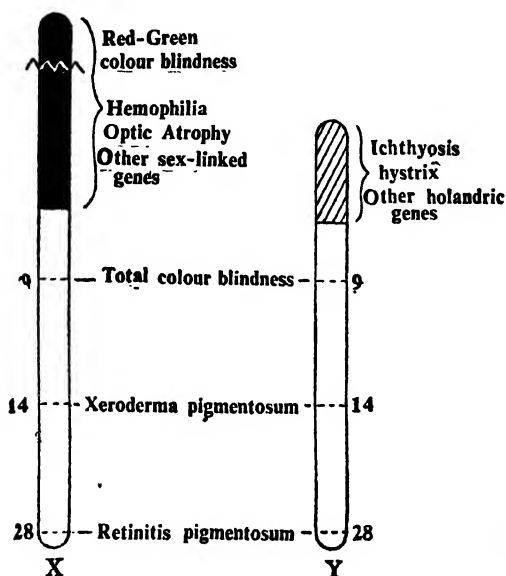


Fig. 11.4 Human sex chromosomes showing some of the sex-linked traits

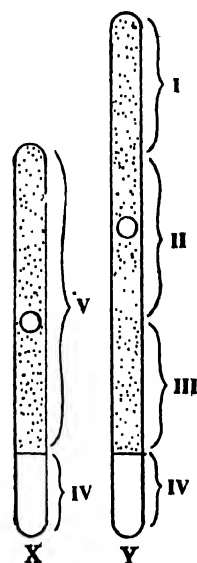


Fig. 11.5 Sex chromosomes of *Melanodrium* where ; I. Female suppressor region, II. Male promoting region, when absent the plant is female, III. Male fertility region. IV. Pairing region, V. Differential region

Several genes are found to be present in this region which are responsible for eight defects in human traits. These include the genes responsible for total colour blindness, xeroderma pigmentation (a skin disease of pigment patches and cancerous growth on the body); retinitis pigmentosum (a progressive degeneration of the retina accompanied by deposition of pigment in the eye) and a type of nephritis (a kidney disease).

CHAPTER 12

Sex Determination

Sex determination is not a problem in case of monoecious organisms as no distinction between males and females exists there. Sex determination of this type of organisms requires no unusual genic mechanism. Since majority of the higher plants are monoecious, no special problem exists in the determination of sex. But we face the problems of sex determination when we begin to study the dioecious organisms. Though the appearance of sex organs comes late in the life of the dioecious organism, still we must have a mechanism of sex determination as to which of the two types of sexes will make their appearance.

In majority of the dioecious animals however, the distinction of sexes appears in their early life cycle and there is a distinct sexual dimorphism (i.e. where the distinction of sexes clearly evident from external observations).

For centuries, biologists and non-biologists were puzzled by this riddle. Before 1900 literally hundreds of mistaken hypotheses and mild guesses were proposed in vain by different scientists from the different corners of the world to find a solution of this problem. A valid solution of this problem came only after the development of genetics in the early part of twentieth century.

Most of the knowledge available on the mechanism of sex determination came from the excellent work of Bridges, Goldschmidt and Whiting, who have whorled separately with flies, moths and wasps respectively.

Considering all the above facts in mind and since the mechanism of sex determination is not same in all dioecious organisms, we shall consider them separately.

12.1 Sex determination by environment : In some lower groups of organisms the determination of sex is non-genetic and is dependent on the external environment. The genotype of the male and female organisms is similar, but a stimulus from the environment initiates the development of sexes.

Environmentally dependent sex determination is known in the sea worms, *Bonellia* and *Dimorphilus* and in the horsetail *Equisetum*. *Bonellia* is an example of extreme sexual dimorphism. The females are about one inch long, while the males are very tiny and live as parasites in the uterus of the female. Here the larvae that are free living and settle on the bottom of the sea, develop into females, whereas the larvae that settle on the proboscis of a female develop into tiny males. It appears that the proboscis of the female contains a substance of the hormone type which influences the sexual traits of

larvae. In *Dimorphilus* sex determination mechanism is related with the size of the eggs. Large eggs produce females while the small ones males. Similarly, *Equisetum* when grown in a very rich soil condition develop into female plants whereas male characteristics are obtained under poor condition.

12.2 Chromosomal Theory of Sex Determination : In the great majority of dioecious organisms the most common forms of sex-determining mechanisms seem to be chromosomal, caused by differences between two types of sex chromosomes X and Y. The most important types of chromosomal sex determination is described below.

XX-XY Method—*Drosophila melanogaster* illustrates the most common method of sex determination by chromosome which is known as XX-XY method. Male and female gametes each have 4 chromosomes, 3 of which are autosomes. The female gametes carry an X chromosome, half of the male gametes have an X and half a Y-chromosome. The sex in *Drosophila* is determined at fertilization. When an egg unites with a spermatozoid carrying X-chromosome, the zygote with 2X chromosomes develops into a female ; on the other hand when the egg unites with a spermatozoid carrying Y-chromosome, the zygote with XY-chromosomes develops into a male.

Human beings also follow the same XX-XY method of sex determination. Here the egg carries the usual autosomes (22) and an X-chromosome. The sperm on the other hand carries the same autosomal number (22) and either an X or Y. The union of egg with Y-chromosome sperm develops into male while those uniting with X-chromosome sperms develop into females (Fig. 12.2).

The XX-XY method is now considered characteristic of most of the higher animals and occurs in at least some plants e.g. *Melandrium album* (Caryophyllaceae). Cytological studies have shown that the female plants of *Melandrium* contain two X-chromosomes in addition to its normal 11 pairs of autosomes. The male plants however contain an X and a much smaller Y together with normal autosomes (11 pairs). Females or pistillate plants are XX, staminate XY. A similar distribution of hetero-chromosomes has been found in over 50 species of dioecious plants like *Elodea*, *Rumex*, *Humulus*, *Smilax*, *Cannabis* etc.

By using colchicine, Warmke (1946) studied sex inheritance in the polyploid *Melandrium album*. The diploid females have 22 autosomes and 2X chromosomes (22+2X), diploid males have 22 autosomes and one X and one Y-chromosomes (22+XY). Tetraploid plants are of three types : 44+4X females, 44+2X+2Y males and 44+3X and 1Y males. This showed that Y-chromosome in *Melandrium* is definitely sex determining and carries genes for maleness. One Y-chromosome is sufficient, even in the presence of 3X-chromosomes to make the plant into a male. Intersexes (or more precisely hermaphrodite)

in *Melandrium* have been obtained due to fragmentation of the Y-chromosome.

Intersexes and Supersexes in *Drosophila*—In 1922 Bridges first experimentally proved the various combinations of X-chromosomes and autosomes in *Drosophila*. He showed that during first meiosis the two X-chromosomes fail to separate and both the X-chromosomes go to one pole. This gives some eggs with the normal single autosomal genome but with 2X-chromosomes (A+XX) while some eggs with the normal single autosomal genome but with no X-chromosome (A+O). Thus the failure of paired chromosomes to separate into two poles is termed as non-disjunction.

The results of such fertilization is given below (Fig. 12.1)

The XXY flies are perfectly normal females inspite of the presence of Y-chromosome. The flies which receive the Y-chromosome but with no X naturally die, as they fail to receive the genes present on the X-chromosome and complete body cannot develop without them.

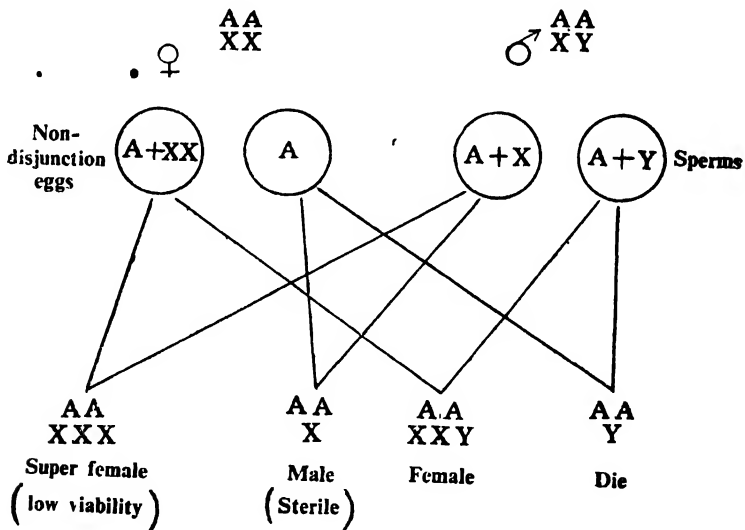


Fig. 12.1 Formation of non-disjunction eggs in *Drosophila* and the results of such union

The fly with XO is a male similar in sex manifestation to XY males, but the former are sterile. XXX flies are called *superfemale* but that does not mean any exaggeration of female characteristics, rather they are sterile and undeveloped in many sexual characteristics. These facts of Bridges clearly suggests that Y-chromosome has got no influence in the determination of sex in *Drosophila*.

Genic Balance Concept of Sex Determination—Another important consideration of sex determination has been made by Bridges who suggested that a ratio between X-chromosomes and autosomes is the

main determining factor in the determination of sex. According to him every individual has in his genotypes both male and female determining factors. In *Drosophila*, X carries more genes which incline the development of the individual towards femaleness and the autosomes more towards maleness. Thus which sex will be actually developed, is decided by the balance of these two types of chromosomes. Different combinations of X-chromosomes and autosomes with sex ratio and corresponding sex expressions in *Drosophila* are shown below :

TABLE-4
Different combination of X-chromosomes and autosomes, and corresponding sex expressions in *Drosophila*

Sex		X Chromosomes	Sets of Autosomes (A)	Sex Index X/A
Super female		3X	2A	1.5
Normal female	Tetraploid	4X	4A	1.0
	Triploid	3X	3A	1.0
	Diploid	2X	2A	1.0
	Haploid	1X	1A	1.0
Intersex		2X	3A	0.67
Normal male		1X	2A	0.50
Super male		1X	3A	0.33

It is evident from the above table that if the ratio of X/A in any individual is 1.0 it will be a female and if 0.5 it is male. When the ratio is intermediate (0.67) between 1.0 and 0.5, the resulting individual is neither a female nor a male but an intermediate or intersex. Superfemales have a ratio of 1.5 and supermales have a ratio lower than the normal male.

XX-XO Method—This type of sex determination is found in grasshoppers and in plants like *Dioscorea* sp. In this type, the females possess even number of chromosomes and the males possess odd number of chromosomes from which Y is dropped. This implies that the females have two X-chromosomes and the males a single X-chromosome. All the eggs of this type carry the X-chromosome but only half of the sperms bear X-chromosome and other half bear only haploid set of autosomes, but no X. Eggs fertilized by the sperm carrying X-chromosome gives a female organism, whereas those fertilized with the sperm without an X-chromosome become males. Here the X-chromosome is the sex influencing agent.

Though the mechanism has been investigated only for few insects and plants, the XO mechanism received wide support in the early part of the present century (Fig. 12.2).

XY-XX Method—This type of sex determination is found in moths, some fishes and in plants like *Fagaria* sp. This is exactly the reverse of the XX-XY method. In this type even number of chromosomes are present in both males and females. The male shows two similar chromosomes (XX) and so they are homogametic (forming only one type of gamete). The females, however, carry

two dissimilar chromosomes (XY) and so they are heterogametic (forming two types of gametes). To avoid confusion with the XX-XY method, this mechanism is often called as the ZZ-ZW method.

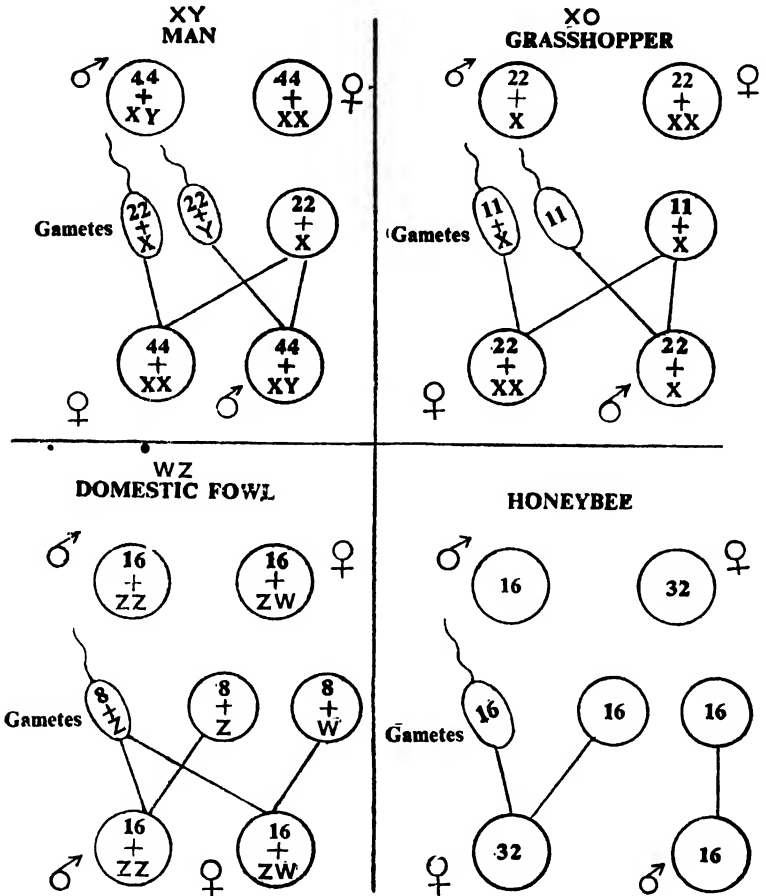


Fig. 12.2 A complete scheme representing the determination of sex in man (XY), grasshopper (XO), fowl (WZ) and honeybee

This mechanism does not imply anything new, but differs from XX-XY method only in that the sexes are reversed (Fig. 12.2).

XO-YO Method—This method of sex determination was first observed by Allen in *Sphaerocarpus* (Bryophyta), where the male gametophytes have 7 autosomes and a small Y-chromosome, while the female gametophytes have 7 autosomes and a large X-chromosome. After gametic union, a zygote is formed with 14 autosomes and one X and one Y-chromosome. This asexual sporophytic body through

reduction division produces the haploid spores carrying only one of the sex chromosomes. This matures into male or female gametophyte depending on which of the two sex chromosomes it receives. In liverworts X and Y are responsible for femaleness and maleness in different gametophytes, whereas the organ with XY is the asexual phase of the cycle (sporophyte). The method of sex determination in *Sphaerocarpos* can be represented in Fig. 12.3.

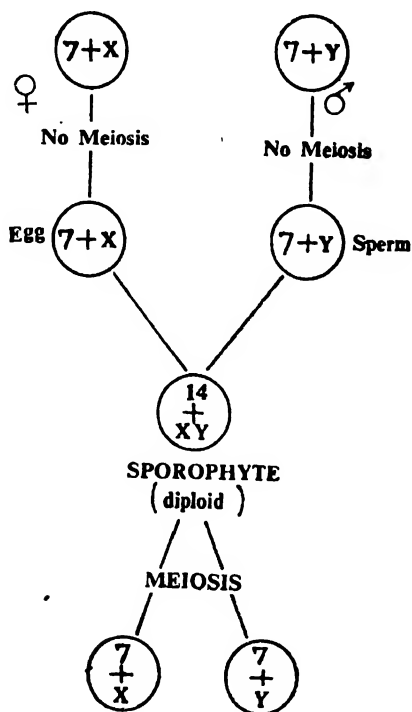


Fig. 12.3 Sex determination in *Sphaerocarpos* (Bryophyta). Meiosis occurs before the production of male and female organisms rather than after as in the majority of plants and animals

Cytoplasmic Inheritance or Extranuclear Inheritance

Since it is an accepted fact so far that deoxyribonucleic acid (DNA) is the basic genetic material and localised practically in almost all the chromosomes, it can be predicted definitely that hereditary transmission of a particular character is mainly tied to the behaviour of the nucleus or more specifically to the chromosomes.

But in the history of genetics there is considerable evidence where the cytoplasm seems to determine the inheritance directly. Although the exact cause of these types of inheritance has not been explained differently, but the evidence indicates the existence of cytoplasmic DNA which is considered to be the information carrying material. *Cytoplasmic or extra chromosomal inheritance will therefore be defined as the inheritance based on the independent hereditary units or materials of the cytoplasm.* Some cytoplasmic factors however, are self-perpetuating i.e., effect not dependent on nuclear genes and are transmitted independently. As they are situated outside the chromosomes, these factors may also be defined as 'plasmagenes', 'plasmons' or 'plasmids'. Another, confusing term is the *maternal effects which may be defined as the effects arising in some way from the genes or tissues of the mother.* They are transmitted through the egg and are not controlled by the genes of the developing embryo.

The difference in the results of the reciprocal crosses is the main criterion in distinguishing extra nuclear inheritance and inheritance of nuclear genes. When the crosses are made between two different species of plants ; in one case species *A* is considered as female and species *B* as male and in another case species *B* is considered as female and *A* as male (i.e. $A \times B$ and $B \times A$), a difference in the results is obtained. A difference in the cytoplasm of the eggs from the two kinds of mother might cause the differential results in the reciprocal crosses. And when such results are detected, an extra-nuclear inheritance or maternal effect can be detected.

13.1 Maternal effect : Since a difference in results is expected in the reciprocal crosses, the eggs or embryos must be influenced by the maternal environment in which they develop. Certain potentialities of the eggs therefore, develop before fertilization. The results of such influences when they can be detected are called **maternal effects**. A number of cases of maternal effect has been studied of which the most important is the pigment formation in the flour moth (*Ephestia kuhniella*). Flour moth has dark brown eyes which is due to *kynurenine*, a pigment precursor formed in the tryptophan metabolism. The appearance of *kynurenine* is controlled by a pair of alleles, *A* and *a* in Mendelian pattern. When a cross is made between a male heterozygous *Aa* with *aa* recessive female, the offsprings appear in the ratio of $1Aa : 1aa$. Phenotypically the larvae will be in the

ratio 1 pigmented : 1 non-pigmented and the mature fly will be dark-brown and red-eyed individual. In the reciprocal cross (*Aa* female and *aa* male), all larvae are pigmented, although when they mature, one half of them are dark-brown and the other half are red-eyed. The egg cytoplasm contributed by the heterozygous mother is therefore responsible for the appearance of pigmented larvae. The eggs of the dark-brown-eyed female contain kynurenine and so there is a development of pigmented larvae irrespective of their genotypes. Half the progeny are *Aa* and therefore continue to synthesize kynurenine and so the adult flies are dark-brown. The other half are *aa* and therefore unable to synthesize kynurenine and consequently developed into red-eyed flies as the kynurenine is used up.

In some cases the maternal effect can continue throughout the life cycle. The best example of such an effect is the direction of coiling of snails (*Limnaea peregra*). Some strains of this species coil to the left (*sinistral*) and some coil to the right (*dextral*). The direction of the shells is characterised by the genotype of the maternal snail. The gene *D* for right-hand coiling is dominant over its allele *d* for coiling to the left. In a cross between a dextral (*DD*) and a sinistral (*dd*), F_1 snails are all coiled to the right. The usual Mendelian 3 : 1 ratio is not obtained. The expected phenotype for *dd* is not expressed, instead the phenotype of the mother's gene is expressed. When these F_2 snails are inbred separately only *dd* progeny coiled to the left while other coiled to the right.

In the reciprocal cross, however (Fig. 13.1) all F_1 progeny are coiled to the left while the F_2 are all coiled to the right. In inbreeding, the F_2 progeny with *dd* genotype produced progeny which coiled to the left. These are clear example of maternal effect.

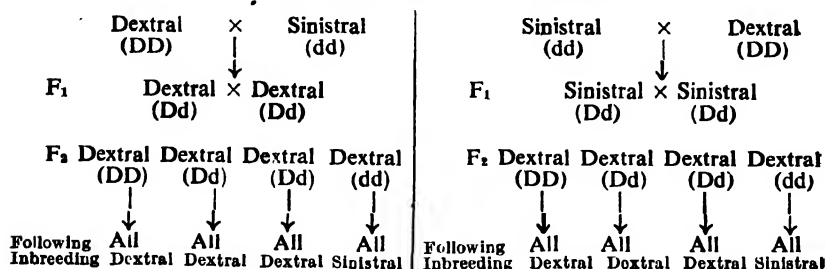


Fig. 13.1 Diagram illustrating the maternal effect in the inheritance of coiling in *Limnaea peregra*

13.2 Extranuclear Inheritance : Like maternal effects extranuclear inheritance can be predicted from the differences in the results in the reciprocal crosses. Here also the traits are not expected according to Mendelian ratios. Most important difference of the extranuclear inheritance is that, the extranuclear factors do not disappear after one generation like maternal effect, but they usually persist as long as this factor perpetuate itself.

PLASTID INHERITANCE IN PLANTS—One of the earliest discoveries of extranuclear inheritance is the plastid characteristics in plants discovered by Correns in 1909. In four O'clock plant (*Mirabilis jalapa*) there is a variety called 'albomaculatus' with variegated leaves (i.e. patches of green and white) in addition to its normal green plant. In crosses between green plants, the offsprings remain green throughout subsequent generations. Crosses from branches wholly white give white progeny (pure white plants die for want of chlorophylls). Variegated branches when crossed yield three kinds of offsprings green, white and variegated. In all the above cases the inheritance is maternal as pollen has little or no cytoplasm. The phenotype thus depends on the factor within the cytoplasm of the egg which is self perpetuating.

In *Mirabilis* this extranuclear factor is the chloroplast containing the green chlorophyll.

Experiments of Correns and others clearly indicate that there is a genetic continuity between chloroplasts like genetic continuity between nuclei. Recently Ris (1962), Chum (1963), Edelman *et al* (1965) and others have demonstrated that the chloroplasts have their own DNA and so a change of chloroplast structure is transmitted in a similar fashion as do nuclear gene. Since the chloroplasts are found only in the cytoplasm, their transmission to new generations mainly occurs through the maternal gametes.

In the inheritance, cytoplasmic factor is not completely dependent of the nucleus, but some relationship exist between the nucleus and the cytoplasmic factor. In corn (*Zea mays*), the *iojap* gene when in a recessive homozygous state gives rise to green and white striped plants. A reciprocal cross between striped plants (*ij/ij*) with normal green individual (*Ij/Ij*) exhibits a peculiar maternal inheritance as found in 'albomaculatus'. This is due to mutation in the plastids thus making them unable to produce chlorophyll. Mutation is stable and when it occurs, its transmission is not modified by the nuclear gene. Thus here the initial determinant is not the plastids but some other factors affected by the *iojap* gene. So it is a typical example of nucleocytoplasmic interaction leading to genetic autonomy of the cytoplasm.

MALE STERILITY IN PLANTS—Another important extranuclear inheritance is the male sterility in plants. In flax (*Linum* sp.) there is a variety known as procumbent and some are erect. Both of these varieties are fertile. Reciprocal crosses between these two varieties of *Linum* give all fertile F_1 plants. In the first cross however where procumbent is taken as female and erect as male, 25% of the plants are male sterile in the F_2 generation, possessing anthers that do not bear any pollen or even do not dehisce. In the other cross where erect is taken as female and procumbent as male, all F_2 plants are fertile.

The probable explanation of the 25% male sterile plants is that they contain a homozygous recessive 'm' factor which induces male

sterility when it is combined with the cytoplasm of the procumbent variety. Since cytoplasm is only transmitted by the egg and not by the pollen, 25% plants of the first cross is male sterile (Fig. 13.2).

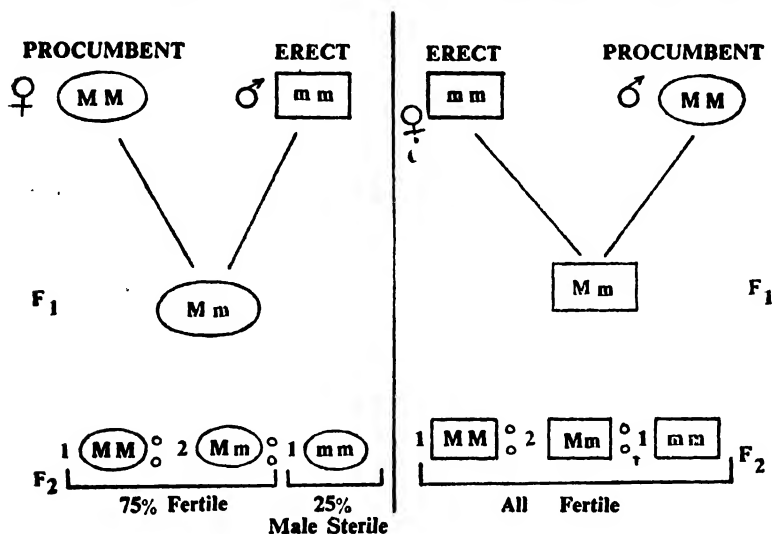


Fig. 13.2 Diagram showing the reciprocal crosses between procumbent and erect varieties of *Linum*

Sterility in maize, sugar-beets, onions and some other plants is also controlled by cytoplasmic factors. In maize, a single dominant gene is known to restore pollen fertility even in the presence of cytoplasm which would ordinarily result in sterility. Thus the cytoplasmic factor is not entirely independent. The male sterility may be wholly gene controlled or may result from the interaction between the genes and the cytoplasm.

Renner and Michaelis regard the evidence from *Epilobium*, a member of Onagraceae as strongly indicative of a hereditary vehicle in the cytoplasm. Wettstein from his extensive studies on mosses has led to similar conclusions.

In spite of the cases cited and additional examples of a similar nature in other plants suggesting a form of cytoplasmic inheritance, this phenomenon must be considered rare in the plant kingdom as a whole.

KILLER PARTICLES IN PARAMECIUM—Cytoplasmic inheritance has been studied on *Paramecium aurelia* by Sonneborn (1943). The unicellular *Paramecium* is a small protozoan which reproduces asexually by fission and sexually by conjugation. During sexual union a temporary cytoplasmic bridge develops through which nuclear materials are exchanged and recombinations of genes occurs.

In course of study it was found that certain races of *Paramecium aurelia* can kill other races when grown in the same culture medium. The strain which kills the other races is called killer trait and the strain which dies is called sensitives. Therefore the strains of *Paramecium* should be of killer or sensitive types. A protozoan antibiotic called paramecin is liberated from the killer race which during conjugation forms a large cytoplasmic bridge, through which cytoplasm is transferred and exchange of nuclear material takes place and is a case of cytoplasmic inheritance. In some rare cases during conjugation, exchange of cytoplasm takes place and by means of which some 'kappa' comes in to the cytoplasm of the sensitive type. If they can receive kappa particles in their body then the protozoan becomes a killer.

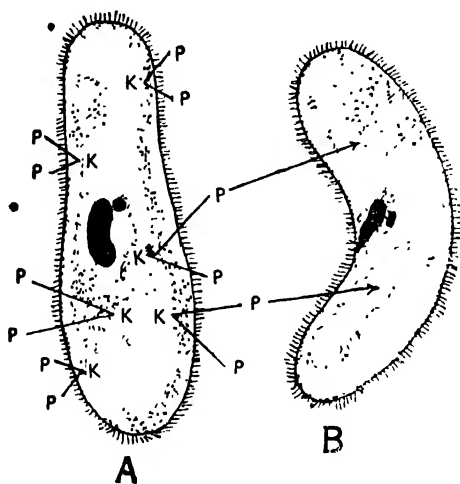


Fig. 13.3 Diagram showing killer and sensitive strains of *Paramecium*
K = kappa. P = paramecin

The substance which generates the paramecin is the 'kappa' situated in the cytoplasm and contains deoxyribonucleic acid. Killer strains possess many 'kappa' particles in the cytoplasm but the sensitive strain is devoid of such particles. Once 'kappa' is lost, it cannot be regained unless and until more 'kappa' is introduced from another cell.

The gene required for the replication of 'kappa' is K. The killer animals should possess in their cytoplasm a particulate element and for the establishment of a killer trait that particulate element should be transmitted. The transmission of 'kappa' particles in *Paramecium* shows the cytoplasmic inheritance (Fig. 13.3).

CHAPTER 14

Objectives of Plant breeding

Plant breeding is a branch of applied Botany and deals with the improvement of crops and plants useful to man through production of new crop varieties which are far better than original types in all aspects. It is therefore "the art and the science of changing and improving the heredity of plants."

14.1 Aims and objective of plant breeding : The following are the aims and objectives of plant breeder for the improvement of plants.

- (i) Improvement of food supply and to increase the rate of production which can be achieved by better cropping practices which yield more productive varieties of crop plants.
- (ii) To prove the quality of the crop plants and the quality of fruits. The colour of the fruit size, flavour, vitamin and juice content etc. can be done by breeding.
- (iii) Resistance to disease and insect pests and also winter hardiness. In crops like tomato, potato, wheat, sugarcane varieties have been produced which are resistant to disease like wilt, blight, rust and red-rot respectively.
- (iv) Production of hardy varieties which can stand against dryness and frozen dew i.e. which can grow in special climatic and soil condition.
- (v) Production of new varieties of crop plants which can resist temporary habitation.
- (vi) Production of new varieties for delight and efficacy.

Before breeding work of any plant, every plant breeder should know the life cycle of that plant in detail and should also know the following points.

- (a) Floral structure and process of reproduction.
- (b) Growing condition of the plant and the environments in which they grow.
- (c) Geographic distribution of the plant.
- (d) In the group the source of variability which can occur due to favourable mutation, from which by means of selection and crossing of the new kind of plants, improved variety may be produced.

CHAPTER 15

Methods of Plant breeding

15.1 Methods of Crop Improvement : The main objects of plant breeding are to produce new crop varieties superior in all aspects as compared to the existing types. This object is achieved mainly through the following methods of crop improvement.

- (1) Plant introduction and acclimatization
- (2) Selection
- (3) Hybridization, and
- (4) Mutation breeding

1. Plant introduction and acclimatization : Variation is the very basis of selection. So, when there is a great variability there is a better chance of selection. Local varieties do not contain all the variability in a single species. It is, therefore, desirable to introduce new materials from other parts of the world to tap all the possible sources of variation in the species. *This method of acclimatizing and establishing the desirable variety in the new environment is termed as introduction.* Acclimatizing on the other hand is the adaptation or adjustment of an individual or a group of plants under changed climates for a number of generations.

The introduced plants may exhibit poor performance during the first two or three years and then they can survive as good healthy types as they exhibited in their native area. On the other hand, the introduced plants may give good result during the first two or three years and then suddenly deteriorate. So, one of the most important factors of introduction is the acclimatization. That is why the new introductions are grown in different environmental conditions for adaptation and to record their performance before selection. Heterozygous types have got better chance of variability than the homozygous pure lines and so the heterozygous types are well introduced than the pure lines.

In early days plant introduction in India was haphazard. There were no organised agencies for introducing plants from outside India. The missionaries, travellers, explorers, colonists, scientists played important roles in introducing new plants from distant countries into India.

These uncontrolled plant introductions in the past are responsible for the introduction of many new weeds, harmful insect pests and diseases with the introduced materials. But gradually with the improvement of scientific knowledge and establishment of several scientific agencies it is now possible to introduce plant material in a more scientific way.

As a result of introduction and acclimatization entirely *new crops*, which were absent in the country, may be grown and brought under widespread cultivation. The superior characters possessed by the introduced material, which are not available in the local ones can be incorporated into the local varieties to boost up the production.

The great advantage of plant introduction is the *easiest method of crop improvement in plant breeding*.

Introduction has an important role in the improvement of agriculture throughout the world. Many of the agricultural crops of India like chillies, castors, sorghums, squashes, pumpkins etc. have been introduced in the early times ; whereas the crops like tea, coffee, cotton, tobacco, potato etc. have been introduced in recent years.

Introduction may take place *directly from introduced stock*. The most important examples of such an introduction are rice strains, *Taichung Native-1* (TN-1) introduced from Formosa and *I.R.-8* introduced from Philippines. *Ridley*, a wheat variety introduced from Australia ; *Sonora-63*, *Sonora-64* and *Lerma Rojo* are the Mexican wheat varieties introduced in India and are very popular among the hill farmers.

Introduction can also be made from *selections of the introduced materials*. The fruitful results of such selection are *Pusa lal* and *Pusa sunehari* varieties of sweet potato, *improved Ghana* variety of bajra and *Pusa basmati* variety of vegetable cowpea.

Introduction can also be made from *hybrid offspring of introductions crossed with native varieties*. Almost all N.P. wheats and hybrid maize varieties released in recent years have some of the superior characters incorporated from the introduced varieties.

2. Selection : One of the important processes in plant breeding is *selection* by means of which plant improvement can be done. Selection means *choosing of superior types from the inferior ones out of the heterogenous mixed types*. There are three general methods of plant selection :—

- (i) Mass selection,
- (ii) Pure line selection, and
- (iii) Clonal selection.

(i) *Mass selection* : It is the most common type of selection and the simplest and oldest method of crop improvement. It consists of picking up a group of best and vigorous plants from the field and harvested together. The mixture of seeds is then sown *en masse* for raising the next generation crop and selection made therefrom. This process is continued till uniformity in the desired characters is obtained. *Mass selection is therefore a procedure of selecting a number of plants phenotypically superior in desired traits from the field, harvesting and bulking together for the next year's sowing and repeating this process till the desired characters are obtained uniformly.*

Mass selection is generally adopted in cross-pollinated plants. It actually takes about eight years to produce a new variety. In the first year the seeds of the desired plants are harvested and preserved for raising crops in the next year. In the second year *preliminary yield trials* are made in isolated plots. The best performers of this trial are kept and the rest are discarded. The *yield trials* are carried from third to fifth year to determine the performance of superior mass selected strains. *Trials on the cultivators' plots* are conducted for three consecutive years (i.e. 6th to 8th year) to determine the adaptability of the strains in the different regions. In the eighth year *the variety is released and named*. The seeds are then multiplied and distributed to farmers for general cultivation.

In spite of certain limitations, mass selection is the most common method of crop improvement among farmers. Majority of cultivated and local strains are the result of mass selection.

(ii) *Pure line selection* : The term "pure line" was first coined by Johannsen in 1903. *It is a strain made up of the progeny of a single self-fertilized homozygous individual*. Pure line plants are homozygous and therefore they are phenotypically or genotypically identical and are uniform in all characters except some minor differences which arise due to variation in the environmental conditions.

Production of pure lines in self pollinated crops occur naturally as they are generally homozygous. The cross-pollinated plants are subjected to controlled self-fertilization for a number of consecutive generations to obtain the pure lines. Repeated self-fertilization in successive generations results in the elimination of heterozygosity and making the population homozygous. *The production of pure lines in cross pollinated plants are known as inbreds*.

Pure line selections are commonly used to improve self-pollinated crops. It consists of selecting a large number of single plants, growing their progeny separately in the field trials and sowing the valuable progeny as a new variety. It is therefore *a process of isolating a desirable homozygous individual from a mixed population and multiplying the same without contamination to produce a new variety*.

Pure line plants may be used as new improved varieties as in self-pollinated plants or as the parents in hybridization programme as in cross-pollinated plants.

The main advantage of the pure line selection is that it is the only method to improve the local varieties of self-pollinated crops. It is further easier than the hybridization in self-pollinated crops, because, here no emasculation and crossing are involved. The varieties produced by pure-line selection are highly uniform in appearance and therefore, are more attractive. Further, it can be used in self- and cross pollinated crops for production of pure lines and inbreds.

The main disadvantage of pure line selections is that there is no possibility of introducing new characters and further since they are homozygous, they are not adopted to large areas under varying environmental conditions. Further if an inbred line is produced the farmer can not maintain it as they are quite unaware of how to control the pollination and so the varietal purity is lost. Great care, attention and labour are to be paid for self pollinating a cross-pollinated crop.

(iii) *Clonal selection*: Due to failure of seed production in many fruits and vegetables like sugarcane, potato, banana etc propagation is usually effected by the use of vegetative parts. Even in many cases like mango, orange, apple etc. where seed formation occurs, but due to wide heterozygosity and high degree of polyploidy, there is a great variation in the population resulting in poor production. Being heterozygous they do not breed true and so purity of race is not maintained. On account of these difficulties these crops are usually propagated by their vegetative parts. *All the progenies of a single plant obtained vegetatively are known as clone.*

Since all the individuals of a clone are in fact obtained from a single plant, they are genotypically and phenotypically identical. The genetical constitution of a clone depends upon the genotype of parental plant.

Clones are quite stable as no variation or segregation occurs in them in their subsequent generation. The clonal population being genotypically alike and direct descendants of a single plant are similar to the pure lines. They, however, differ in two fundamental aspects. First, the pure lines are genetically alike (except mutation) and are homozygous while the clone though genetically alike are always heterozygous. Second, repeated self fertilization in a heterozygous plant result in the production of a number of pure-lines whereas only one clone is produced by repeated vegetative propagation from one heterozygous plant.

The main advantage of clonal selection is that the varieties are stable and easy to maintain. If a plant with hybrid vigour is obtained it can be easily preserved by this type of selection.

The main limitation of this type of selection is that this method is applicable only to vegetatively propagated crops and further it does not produce any new variation.

3. Hybridization: One of the most important method of plant breeding is hybridization. *It is the method of producing new crop varieties in which two or more plants of unlike genetical constitutions are crossed together.* The different plants which are crossed in this method may belong to the same species, different species or different genera. Depending upon the parents involved, hybridization is of the following types: (a) *intra varietal hybridization*, (b) *intra specific hybridization*, (c) *inter specific hybridization* and (d) *inter generic hybridization*. Among the above four types

of hybridization intra- and inter-varietal hybridization are of common occurrence in nature than the other two types. Intra- and inter-varietal crosses can be easily done with almost cent percent success while the others, though artificially practised, result in very little success.

The main aims of hybridization is,

- (i) to combine all the possible good characters in a single variety,
- (ii) to increase the genetic variability by introducing various recombinations of characters and
- (iii) to exploit and utilize the hybrid vigour¹

15.2 Hybridization Procedure : Hybridization process is a very technical operation and requires a very skilled hand. The various steps involved in the process are as follows :

(a) *Selection of parents* : The first step in hybridization is to select the plants which should be used as parents. Care should be taken that the parents contain all the desirable characters which are lacking in a standard variety. Usually the parents should be healthy and vigorous. The plants should be checked against any contamination of foreign pollens and disease. Only the plants with desired characters should be selected as parents.

(b) *Selfing of parents* : It is the second step of the process where the parents are artificially self-pollinated. This process is very essential in order to eliminate the undesirable characters and obtaining inbreds.

In case of self-pollinated plants selfing can be automatically done if they follow their natural mode of pollination. If the natural cross-pollination is slight it can be ignored, if however, it is excessive, the flowers must be protected by bagging so that selfing automatically takes place inside the bag.

In case of cross-pollinated plants the process of selfing is very cumbersome and the parents are artificially selfed. Depending upon parents there are different ways of artificially selfing the parents. In case of dichogamous plants like *bajra* (*Pennisetum typhoides*) the panicles are simply bagged and self-pollination takes place automatically inside the bag. But in case of monoecious plants like maize (*Zea mays*), both male and female flowers are bagged separately before the dehiscence of anthers from the tassels (male inflorescence) and emergence of silks from the cobs (female inflorescence). After the emergence of silks they are pollinated with the pollen of bagged male inflorescence of the same plant.

(c) *Hybridization technique* : Since the inbred plants are less vigorous and low in yield, they cannot be released directly for cultivation rather they are combined together by hybridization technique. The inbred plants are grown in isolated plots with all

1. For detail refer chapter 16, *Hybrid vigour*

proper care against disease and pests. The following operations are carried out.

1. Emasculation : It is the third stage of the hybridization process where the stamens are removed from the female parent before the anthers are mature. *Thus the removal of stamens from female*

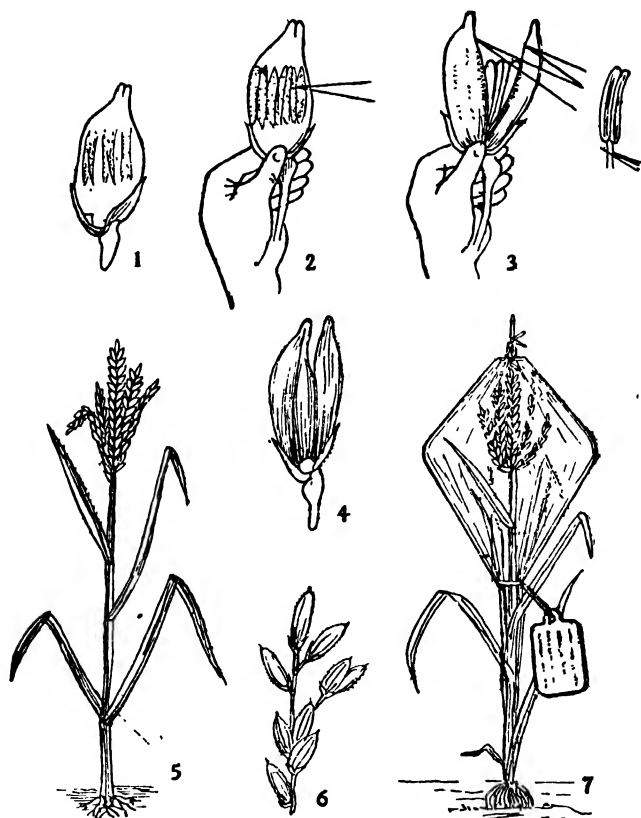


Fig. 15.1 Hybridization techniques in rice. 1- 4. showing emasculation in rice. 5. rice plant. 6. inflorescence of rice. 7. to prevent cross-pollination rice plant is covered with plastic bag and labelled

parent before they burst and have shed their pollens is termed as emasculation. Emasculation is however not necessary at all in case of unisexual plants, but it is a must in case of self- or cross-pollinated bisexual plants. The following are the different methods of emasculation.

(i) **Forceps or Scissors method :** It is a process where the opening of flowers and removal of anthers are done with the help of forceps or scissors. This is generally done in case of plants which bear large flowers.

(ii) *Hot water emasculation* : In plants like rice, sorghum, bajra etc, where the flowers are very small, the whole panicle is dipped in a bottle containing hot water having a desired temperature for a definite period. The following is the method of emasculation in rice adopted by Jodon. Warm water ($\pm 45^{\circ}\text{C}$) is taken in a thermoflask and the mature panicle is kept immersed for 10 mits. Thus the temperature renders all the anthers of the flowers sterile.

(iii) *Male-sterility method* : In case of plants like sorghum, barley, onion, bajra etc the whole operation of emasculation is eliminated by the use of male-sterile plants (i.e. which have sterile anthers and do not produce any viable pollens). Male sterility may be due to cytoplasmic or genetic cause. It can be induced by the application of some chemicals like 2, 4-D, NAA, maleic hydrazide etc.

2. **Bagging** : After emasculation, the male and the female flowers are bagged separately with plastic, muslin or paper bags in order to prevent contamination in staminate flowers and cross pollination in pistillate flowers. The pollens collected from the bagged males are then used for pollinating the female flowers.

In case of males the bags are removed as soon as the crossing is over, but they are however kept as such on the females till seed setting is complete. In some cases the bags are punctured with numerous holes to allow ventilation and prevent mould development inside the bags.

3. **Crossing** : It consists of collecting the viable pollens from the desired male parents and transferring them on the stigma of desired emasculated female parent. The pollens from the bagged male parent are collected in petridishes or in paper bags after dehiscence of the anthers. The bag is the temporarily removed from the female parent and the collected pollens are then brushed or dusted on the stigma. After crossing the female parents are again bagged.

Crossing should be done in appropriate time i.e. when the anthers dehisces and the stigmas are receptive. In most crops the stigmas are receptive in the morning hours and so crossing at that time is most effective.

4. **Labelling** : Immediately after crossing the crossed flowers should be tagged and labelled. Labelling can be done either on the bag itself or on the tags (labels). The labelling should be short but informative; like reference number of the field, date of emasculation and crossing and details of parents etc. Other necessary particulars must be entered in a handy field record book and the observations are also recorded from time to time.

(d) **Harvesting the hybrid seeds and raising F_1 generations** :

It is the last stage of the process where after removing the bags, the seeds are collected separately in a labelled envelope. After

proper drying they are preserved carefully. In the next season the seeds are sown separately to raise the F_1 generation.

15.3 Hybridization method : The seeds of F_1 generation and subsequent generations are then collected by different selection methods of hybridization. For self- and cross-pollinated plants the methods adopted are given below :

Self-pollinated crops

The different methods adopted for self-pollinated crops are as follows :

(a) *Pedigree method* : From F_2 populations, the individual plants are selected on the basis of desired characters. The seeds of the *selected plants are harvested and threshed separately*. The seeds are sown in the next year to raise the F_3 generation. The same procedure is followed upto F_6 generation. The plants of uniform desired characters are harvested and bulked together to constitute a variety.

This method is very expensive as the breeder have to pay more attention and labour for keeping the clear pedigree records of each selected plant separately in the early generations.

(b) *Bulk method* : Here the F_2 plants *are not maintained separately* but are bulked together to form a single F_2 population. In F_3 generation the seeds of the selected plants are collected and bulked together. This procedure is followed upto F_6 generation.

This method is very simple, convenient and inexpensive. It minimizes the labour as the breeder does not to pay individual attention.

(c) *Back cross method* : This method is usually employed for improving self- and cross-pollinated crops particularly by transferring one single inherited characters like disease, frost or drought resistance, earliness etc. from an undesirable variety to a good commercial variety. Here the F_1 plants (instead of self-pollinating as done in pedigree or bulk method) are crossed with the parent. The back cross progenies are again back-crossed upto 6th generations after which the selected plants are self-pollinated to make the population homozygous for that particular desired characters.

This method is very advantageous as it is a very quick process and quite independent from environment. Further it does not require any agronomic performance i.e. the back cross derived varieties can be safely released to the cultivators without any cultivators' trial.

(d) *Multiple cross method* : It consists of crossing several pure lines together. In first generation the pure lines are combined together in crosses as $A \times B$, $C \times D$, $E \times F$ and so on. F_1 of these crosses are then combined into double crosses as $(A \times B) \times (C \times D)$. This cross is known as **multiple cross**.

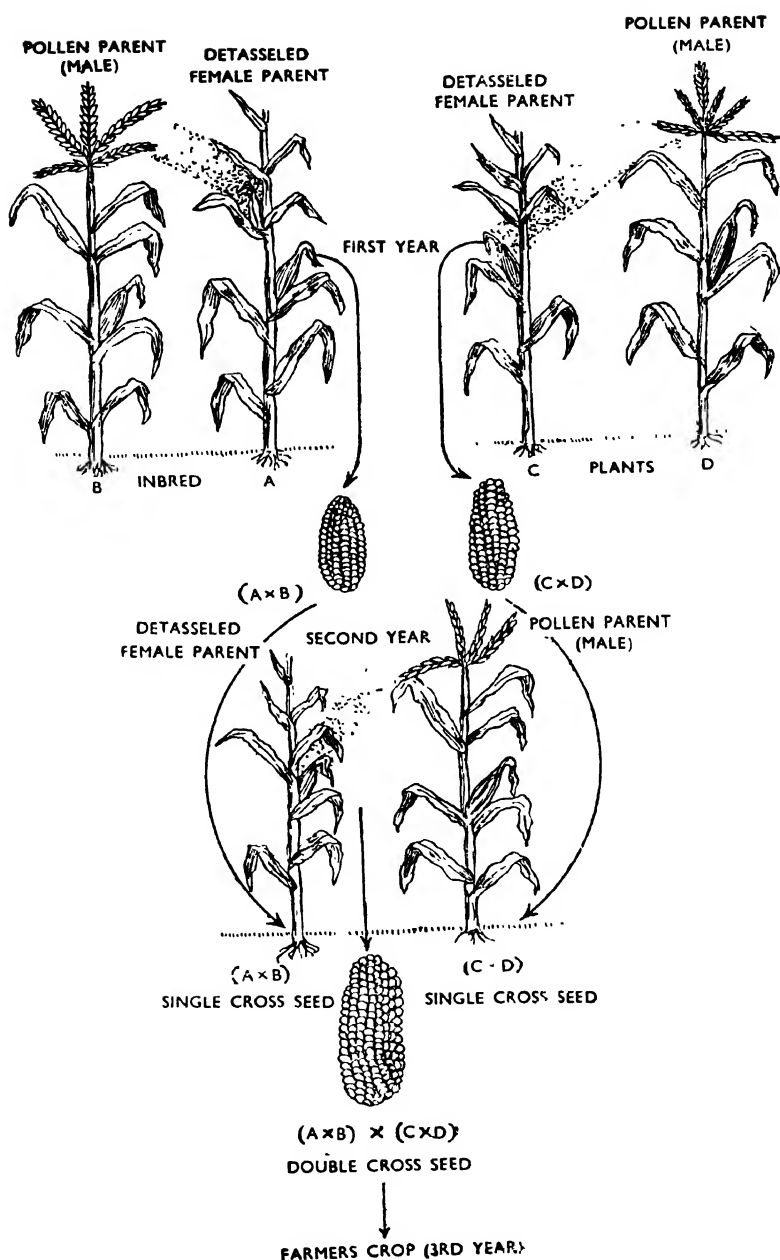


Fig. 15.2 Methods adopted for obtaining double cross-seed in corn (maize)

Cross-pollinated crops

The inbreds obtained earlier are combined as any one of the following method and released as improved strains.

(a) *Single cross* ($A \times B$): It consists of crossing two inbreds i.e. $A \times B$ or $C \times D$. The hybrid seeds are distributed to the farmers for raising the crop. This is done by planting two female lines to one male line alternately. It produces maximum degree of hybrid vigour and produces most uniform plants and ears. On the other hands, the kernels are very small in size and the seeds are poorly developed. It involves high cost of seed production and therefore commercially undesirable, but they are utilized as a foundation hybrid for double or three-way crosses.

(b) *Three-way cross* [$(A \times B) \times C$]: It is a cross between a single cross ($A \times B$) taking as a female and an inbred line (C) as a male. Since here the hybrid of first generation is taken as a female, the yield of hybrid seeds is maximum together with the normal kernel size.

(c) *Double Cross* [$(A \times B) \times (C \times D)$]: It consists of crossing two single crosses involving four inbred lines. Two similar or closely related inbreds are usually combined in the single cross and different or distantly related inbreds in the double cross.

Majority of the commercial hybrids are the results of double cross. All the hybrid seeds of maize (*Zea mays*) distributed to farmers for cultivation are the results of double cross. They give a very high yield without increasing much the cost of production.

Production of hybrid maize seeds: By crossing two inbred lines hybrid seeds are produced which can be done by isolating the pure lines. The parent inbreds i.e. male stock (pollinator) and female stock (seed producer) to be crossed are planted in fields alternately. Such plants are separated from other varieties of corn to prevent contamination. Usually the plants are planted with two female rows alternating with one male row. Emasculation is done simply by removing the tassels from the female parent. So the female parent develops cobs on the axils and the male parent develops panicles or tassels on the apex.

The method of producing double cross hybrid is schematically represented in Fig 15.2.

F_1 single cross hybrids are crossed again to obtain double cross seed because the production of single cross grain is low. Hybrid corn seeds are generally produced through double crosses.

CHAPTER 16

Heterosis or Hybrid Vigour

All the progenies of a hybrid do not resemble their parents, rather a cross breeding of two homozygous inbreds of genetically unlike constitutions show more vigorous hybrid offsprings than either of the parental strains. This superiority of the hybrid has been coined by Shull (1914) as **heterosis**. It is also called **hybrid vigour**. Heterosis or hybrid vigour may therefore be defined *as the increased vigour, size, growth or other functions of the hybrid over their parents resulting from the cross of genetically unlike organisms*.

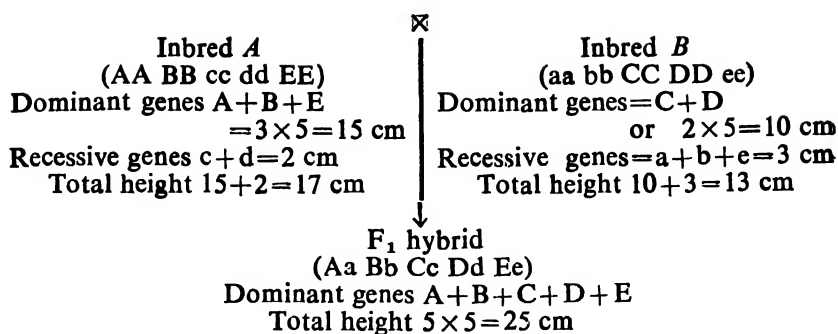
Though both these terms are used synonymously, but Poweri (1945) considers heterosis to include both vigorous or weak hybrids, whereas hybrid vigour refers only to the increased vigour and size.

The major effect of heterosis is **quantitative** particularly in increasing the yield, fruit, vegetative parts etc. Another effect is **biological** which means the increase in biological efficiency of an organism like reproductiveness and survival ability. Another important effect is **physiological** which includes traits like adaptability, disease and insect resistance, earliness etc.

It has been observed that the heterosis from the crosses of distantly related inbreds exhibit more hybrid vigour than those from closely related parents. So inter specific crosses exhibit more hybrid vigour than the intra specific crosses.

16.1 Causes of heterosis : The actual cause of heterosis has long been a debated question. One of the possible cause of heterosis is the superiority of the heterozygotes. This superiority of heterozygotes has been called the **overdominance hypothesis**. Heterozygotes for a single gene difference is obviously superior to either of the two homozygotes. This is due to metabolic advantage of the gene products produced by two heterozygous genes (A/a), rather than by only one kind (A/A or a/a).

Another hypothesis has been termed as **dominance hypothesis**. This hypothesis is based on the fact that dominant alleles are superior whereas the recessive alleles are deleterious. Suppose two inbreds A and B are crossed to produce F_1 hybrids; inbred A has got the genotype AA BB cc dd EE and B has got the genotype aa bb cc DD ee. Suppose here the dominant genes (A, B, C, D and E) each contributing 5 cm towards the height of the hybrid. In the absence of the dominants, each recessive gene contributes 1 cm towards the height :



The above figure illustrates that the hybrid has got more favourable dominant genes and for this reason, it contains more vigorous growth and increased yield than either of its parents.

Although several hypothesis have been proposed for heterosis, at present no clear cut evidence has yet been furnished for heterosis. Some, however, is of opinion that both dominance and over-dominance may operate to produce heterosis (Crow, 1952)

Heterosis has been clearly demonstrated in corn (*Zea mays*) for its marked effect on yield improvement. Heterosis in the F₁ hybrid seed is obtained by crossing inbred lines. At present majority of the improvement in the yield of corn has been made through hybrid corn. Besides corn, hybrid vigour have been successfully employed in sorghum, bajra, wheat, cotton, tobacco, potato, tomato etc.

Hybrid vigour has also been exploited in animals like cattle, poultry pigs, silkworms etc. A careful exploitation of hybrid vigour in cultivated plants and domestic animals may increase the production of food and fibre crops directly resulting in better nourished human race and more prosperous agriculture.

17.1 Introduction and Definition : *Biometry* may be defined as the branch of statistics which deals with the study of biological problems or the application of mathematical methods to the study of living things and organisms. Statistics, as we know, is that branch of applied mathematics which deals with collection of numerical observations and their expression in logical terms or interpretation of the results. The science of biometry was founded by Francis Galton and later on developed by Karl Pearson, R. A. Fisher and others. At present biometry is an indispensable tool in all the branches of biology and specially in agricultural research.

In biology, we deal with living things and no two individuals—plants or animals—are exactly alike. For example, if we record the height of rice plants growing in a plot of land, we would find difference or variation in height among individual plants; though they were grown from the seeds of the same variety and received the same cultural practices. These differences or variations may be large or small. Such variations can not be wholly due to experimental error or error in recording the observations or data. Experimental error is a part of biological variation but not solely responsible for it. The occurrence of variation makes the application of statistical methods in biological sciences, i.e. biometry, all the more important than in the physical sciences. Experimental error is common to both, but in biology the worker has to deal with other sources of variation that are quite distinct. The purpose of biometry is to reach worthwhile conclusions in the presence of variations and “to provide a measure for the probable truth of statements”, which may be applied to the whole groups of individuals, even to all the individuals of a species.

When we conduct any experiment, the data obtained may be either qualitative or quantitative in nature. In the *qualitative* or *enumeration data*, the individuals under consideration are indicated by some quality or attribute, viz. colour of the flower, nature of the seed coat, nature of the endosperm, colour of eye in animals etc. We come across this type of data specially in genetical experiments. Enumeration or qualitative data always involves the number of individuals conforming to a given set of descriptions. Sometimes it may be based on only one criterion (e.g. colour of flower) with several categories (e.g. red, white, green, yellow etc.) or there may be two or more criteria, each with two or more categories. The *quantitative* or *measurement data*, on the other hand, are based on a measurement or count of the individuals, viz. height, weight, yield

of a crop, number of flowers on a plant or number of petals in a flower etc.

Biometry being a branch of applied mathematics use of mathematical formulae and algebraic notations can not be avoided in our study, but before proceeding further, it will be convenient to get acquainted with certain terms which are regularly used in biometry.

POPULATION AND SAMPLE—*A population is a series of numbers that represent some variable, quantitative character being treated as a whole.* A population is usually infinite in size. The sum total of a large number of individuals or units of any one kind, having certain common fundamental characteristics is known as a **population**. In the example of height of rice plants, all the plots of the same soil type and in the same season may comprise the population and which is a hypothetical quantity. It is impossible to measure all the plants for the purpose of statistical analysis. So, in order to make the work possible, descriptions of the population must generally be formulated from **samples** to be drawn from the population. In order to make useful estimates of a population, the samples must be drawn randomly to represent the same type and degree of variability as occurs in the population.

In biometry (or statistics), observations are taken from a sample or samples, but the conclusions are applied to a population. One of the purposes of statistical analysis is to gather useful information about a population from study of the sample. *Actual values for populations are constants called parameters; estimates of population obtained from samples are called statistics.* In biological materials the parameters are very rarely known, so one has to depend on the samples for conclusion applicable to populations.

VARIABLE AND VARIATE—*Any quality or quantity which is likely to vary from individual to individual in the same population is known as a variable.* In the example of rice plants cited earlier, the height is the variable. In any statistical analysis the variables provide the raw materials for work. Two categories of variables are generally recognised, viz. (a) *Continuous variables*—are those which can have any value or fraction thereof and are generally considered as measurable with a scale. Examples are height, weight, length etc.; (b) *Discrete or Discontinuous variables*—are those which can have only a restricted set of values, where the numbers can not take fractional values and therefore must be integers (whole numbers), differing from one another by definite and regular gradations. For example, in counting the number of beans in a pod, we will always find a whole number, i.e. 1, 2, 3, 4, 5, 6, etc., but never 3.25 beans in a pod. Similarly, the number of grains in an earhead of wheat, number of petals in a flower etc. are examples of discontinuous variables.

An individual count, measure or value of any variable is termed a variate. Each of the measurements of height of rice plants is a variate, height being the variable under study.

17.2 Measurement of Variation : In the previous article we have seen that one of the most important purposes of biometry is to provide means for measurement of variation in the material under study. Here it will be shown how this is actually done. In measuring variation certain mathematical formulae and constants are used. Some of the important ones are as follows :—

A. ARITHMETICAL MEAN (or simply Mean)—Which as the term implies, is the mean or average and is found by finding the sum of all the individual observations or measurements and then dividing the total by the number of observations or measurements. The mean is represented by \bar{x} (called x bar) and the formula for finding the mean is ;

Mean (\bar{x}) = $\frac{\Sigma x}{n}$, where x is any single measurement or observation,

n is the total number of observations or measurements in the test, Σ —the Greek letter sigma which signify summation, Σx (called sum of x) = the sum or total of all the observations. An example to clarify the method :

Example 1st : Calculation of mean height of 20 rice plants. The height of 20 rice plants recorded in centimetres were as follows :— 64, 72, 66, 67, 68, 73, 67, 65, 61, 67, 63, 76, 73, 72, 75, 76, 68, 66, 65 and 76.

To find the mean height we use the formula $\bar{x} = \frac{\Sigma x}{n}$ where x represents the individual readings and n the total number of individuals measured. Thus, the 20 readings are summed, which gives $\Sigma x = 1380$, dividing this by 20 i.e. $\frac{1380}{20} = 69$, so the mean height of 20 rice plants $\bar{x} = 69$ cm.

In cases like the above, where the number of observations is small, the mean can be easily found out directly by this formula, but where the number of observations is large, much of the tedious arithmetic can be cut down by grouping the data (*i.e.* measurements or observations) in a manner known as **frequency distribution** and then calculating the mean by a slightly different formula. Let us take the calculation of mean height of 200 wheat plants. After recording the measurements it is seen that the shortest ones are 48 cm and the tallest ones are 58 cm *i.e.* the range of height varies between 48 and 58 cm and all the 200 plants fall within this range. This range can be divided into 6 *classes*, taking a *class interval* of 2 cm *viz.* 48, 50, 52, 54, 56, 58. Division into classes and selection of class interval should be done after a thorough examination of the data. In this particular example there were no fractional measurements and no plants with height intermediate between the chosen classes (*i.e.* 49, 51, 53 etc). Next the number of measurements falling under each class is determined. This is known as the *frequency* (f)

of each class. For example 8 plants have a height of 48 cm and thus fall under that *class value* (x), 32 plants in class value of 50 cm and so on. The sum total of the frequency gives the total number of observations (n). After setting out the class value (x) and frequency (f) in a tabular form, the mean (\bar{x}) is calculated by the formula.

Mean (\bar{x}) = $\frac{\sum(fx)}{n}$, where f = the frequency of individuals in each class, x = class value of measurements and n = the number of individuals in the sample. The actual calculations are shown in the following example—

Example 2 : Calculation of mean height of 200 wheat plants.

<i>Class value (x)</i> cm	<i>Frequency</i>	<i>Frequency</i> × <i>Class value (fx)</i>
48	8	384
50	32	1600
52	75	3900
54	52	2808
56	28	1563
58	5	290
	<hr/> n = 200	<hr/> Σfx = 10,550

$$\therefore \bar{x} = \frac{\sum fx}{n} = \frac{10,550}{200} = 52.75 \text{ cm}$$

It should be remembered, however, that we would have got the same mean if the calculation was done with the previous formula

$\bar{x} = \frac{\sum x}{n}$, but in this case the arithmetic of adding 200 figures is simplified. Please note that in case of samples the mean is denoted by \bar{x} but the population mean is denoted by the Greek letter μ (mu), though the same formula is used for calculations.

If the data from the above example or from even larger samples are plotted on graph paper, with the frequency (number of observations) along the ordinate and the measurements (height in this case) along the abscissa we get a curve which is generally "bell-shaped", with a peak in the middle and tapering down more or less symmetrically with higher and lower values of the variable. Such a curve is known as the *normal curve* or *curve of normal distribution* and is frequently observed for most of the biological characters. A normal distribution curve has three important features, viz. (i) **Mean**—the arithmetic mean or average of the observations and the distribution of values is equal on either side of the mean; (ii) **Mode**—the class of variate which occurs with the greatest frequency or is the class in which there are the highest number of variates. In example 2, 52 is the most frequent class and therefore is the modal class, and (iii) **Median**—the middle value or observation when the variates are arranged in order of their values. In a perfectly normal curve the mean, the median and the mode coincide. Because of the frequent occurrence and regularity of normal distributions, these are very important in biometry but as clear understanding of the nature and properties of the normal curve involves complex mathematics it will not be discussed here any further. Anybody interested in this may consult the standard text books on Statistics and Biometry, some of which have been mentioned in the References.

B. MEAN DEVIATION—*Each value of the variate differs from the sample mean by an amount which is termed its deviation.* The deviation (d) of any observation (x) is expressed by the equation $d = x - \bar{x}$. The deviation may be either positive or negative depending on whether the observation (x) is greater or less than the mean (\bar{x}). The mean deviation is calculated by summing the product of the deviations of observations and the class frequency ignoring the + or - signs and then dividing the sum by the total number of observations. The mean deviation for observations in a frequency distribution is calculated by the formula,

Mean deviation = $\frac{\sum(f.d)}{n}$, where f = the class frequency, d = deviation of the class value from the mean, n = total number of observations and \sum the sign for summation. The formula may also be written as $\frac{\sum(f.d)}{\sum f}$.

The calculations may be shown with data from example 2.

Frequency (f)	Deviation from mean (d) = $(x - \bar{x})$	$f.d.$ (+ or - sign ignored)
8	-4.75	38.00
32	-2.75	88.00
75	-0.75	56.25
52	+1.25	65.00
28	+3.25	91.00
5	+5.25	26.25
<hr/> n or $\sum f$ = 200		<hr/> $\sum f.d.$ = 364.50

$$\bar{x} = 52.72$$

$$\therefore \text{The mean deviation is } \frac{364.50}{200} = 1.822$$

The mean deviation is only a simple measure of variation and does not give much information in statistical analysis.

C. VARIANCE: *Variance is a measure of variation and is the sum of squares of deviations (d) divided by the total number of observations.* The formula for calculation of variance is as follows:—

$$\text{Variance of the sample } s^2 = \frac{\sum f.d^2}{(n-1)}$$

(Variance of the population is denoted by σ^2 —sigma squared).

It may be seen that in the above equation for calculation of variance the total of the squared deviations has not been divided by n (the total number of observations) but by $(n-1)$ i.e. the total number *minus* 1. This is known as the *number of degrees of freedom* and it denotes the number of comparisons that can be made between any one observation and the rest of the observations, taking them in pairs. If there are 20 observations (n), the number of degrees of freedom comes to $(20-1)$ i.e. 19, since only a single observation can be compared with each of the remaining 19 observations taking one at a time. Sufficient mathematical proof

has been provided for using the divisor $(n - 1)$ in the formulae for measurement of variation in statistics, which is out of scope of this text. But it may be mentioned that by using $(n - 1)$ as the number of degrees of freedom we can get an unbiased estimate of the variance of the population σ^2 from the sample variance s^2 . The use of $(n - 1)$ number of degrees of freedom will be found in subsequent topics also.

Example 3 : Calculation of variance of a sample ; for this we shall take up the data from example 2.

Frequency (f)	Deviation from mean $d = (x - \bar{x})$	Deviation squared d^2	Frequency \times deviation squared $f \cdot d^2$
8	-4.75	22.56	180.48
32	-2.75	7.56	241.92
75	-0.75	0.56	42.00
52	1.56	1.56	81.12
28	3.25	10.56	295.68
5	5.25	27.56	137.80
Σf or $n = 200$			$\Sigma f d^2 = 979.90$

$$\bar{x} = 52.75$$

$$\therefore \text{Variance } s^2 = \frac{\Sigma f d^2}{(n-1)} = \frac{979.90}{(200-1)} = \frac{979.90}{199} = 4.92$$

The use of variance (s^2 or σ^2) as a measure of variation is of little help, because it gives the result in terms of the square of the units of measurement. For example, in calculating the variance of the number of flowers in some plants the result is expressed as so many 'square flowers'—which is some thing absurd. So a better way is to use the Standard Deviation.

17.3 Standard Deviation : A statistic measuring the spread or variability of the sample (or population) around the mean is known as the standard deviation. It is obtained from the variance (refer art. 17.2C) by extracting the square root and is expressed in the units in which the measurements are taken. Standard deviation of the sample mean is calculated by the formula

$$s = \sqrt{\frac{\Sigma f d^2}{(n-1)}}$$
 (standard deviation of the population mean is expressed by the symbol σ —sigma).

To give better precision to the mean, the standard deviation is used with a plus over minus sign \pm after the mean value i.e. $\bar{x} \pm s$. From calculation of standard deviation we can get an idea about the extent to which the entire sample (or population) is represented by the mean.

Example 4 : Calculation of standard deviation of a sample.

This will be illustrated with data from example 3.

As standard deviation (s) is the square root of the variance (s^2) we simply find the square root of the latter.

Thus, $s = \sqrt{s^2} = \sqrt{4.92} = 2.21$ cm.

The mean therefore can be expressed as $\bar{x} \pm s = 52.75 \pm 2.21$.

It should be noted, however, that the standard deviation of the sample (s) does not give an unbiased estimate of the standard deviation of the population (σ). So, it is frequently used in case of the infinite population, rather than to samples drawn from that population. But if the samples are large and selected at random, the standard deviation gives a good indication of the variability of the population. The standard deviation tends to increase with the increase in variability of the sample. This has been mathematically established from studies of the normal distribution curve.

17.4 Coefficient of Variation : Another measure of variability is obtained from the *coefficient of variation*—which is the *standard deviation expressed as percentage of the mean*. It is calculated from the formula

C. V. = $\frac{s}{\bar{x}} \times 100$ or $\frac{\sigma}{\mu} \times 100$ in case of samples or populations respectively.

The coefficient of variation, being expressed in percentage, is independent of the unit of measurement making it possible to compare the relative variability of samples (or populations) with widely different means or recorded in different units of measurement. It is used where the other measures of variation can not be used. For example, we can not compare the standard deviation of yield and height of rice plants, because, the former is recorded in grammes or kilogrammes and the latter in centimeters. But it is possible to calculate the coefficient of variation in each case and to state that the relative variability in yield is greater than or equal to or less than the variability in height.

Example 5 : Calculation of coefficient of variation in a sample.

Once again we refer to the data in example 2.

The mean height of 200 plants (\bar{x}) = 52.75 cm and the standard deviation (vide example 4) s = 2.21 cm.

Therefore the coefficient of variation i.e. C. V. = $\frac{s}{\bar{x}} \times 100$

$$= \frac{2.21 \times 100}{52.75} = \frac{221}{52.75} = 4.19 \text{ per cent.}$$

17.5 Standard Error : Another useful statistic for measurement of variation is the *standard error* of the sample mean. While variance and standard deviation measure the variation among individuals under study, *standard error is a measure of the variation of the means*. From standard error we can determine how the sample mean (\bar{x}) is related to the mean of the population (μ) from which the sample was taken. The standard error of the mean can be calculated from the standard deviation (s) of any sample, by dividing it by \sqrt{n} . Thus, the formula for standard error is :

Standard Error $s_{\bar{x}} = \frac{s}{\sqrt{n}}$, where s is the standard deviation of the sample and n is the size of the sample. The standard error is used

after the mean with a \pm sign in between, viz. $\bar{x} \pm \bar{s}$. (S. E. is also expressed as $\frac{\sigma}{\sqrt{N}}$).

The standard error gives an estimate of the variation of several other similar samples drawn from the same population. If the variation in the population is large, a larger sample will be necessary, than when the variation is small. The smaller the standard error the more reliable will be the estimate of the population mean. An increase in the size of the sample (n) results in a decrease of the magnitude of standard error. It is therefore necessary to large samples for determination of the population characteristics.

Example 6 : Calculation of standard error of sample mean.

From the previous example of height of 200 plants.

We have $\bar{x} = 2.75$ cm and $s = 2.21$

\therefore the standard error of the sample mean

$$s\bar{x} = \frac{s}{\sqrt{n}} = \frac{2.21}{\sqrt{200}} = \frac{2.21}{14.14} = 0.156$$

We can express the mean and the standard error

$$\text{as } \bar{x} \pm s\bar{x} = 2.75 \text{ cm.} \pm 0.16$$

17.6 Test of Significance and "t" test : The method for calculating the probability of obtaining an observed result from some hypothesis and regarding the hypothesis as rejected or not is known as a **test of significance**. If the probability is not greater than some pre-selected value, the observed result is said to be *statistically significant* at the chosen level of probability. If, on the other hand the probability is greater than that selected as the "dividing line". The result is considered to be *not significant* at the chosen level, the probability selected for the test is called the *level of significance*. In biological and agricultural experiments, generally, a probability of 0.05 or one chance in twenty is taken as indicating that there are reasonable grounds for rejecting the hypothesis under test. In other words, "if the probability of obtaining a deviation from the hypothetical value as large as or larger than that observed is 0.05 or less, we consider the deviation to be significant." The probability of 0.05 is also referred to as 5% level of significance.

In making a test of significance the following steps are usually followed : (a) a hypothesis appropriate to the problem is set up—this is known as *Null Hypothesis*. It is merely what is expected to occur according to some standard scientific theory. For example in comparing the means of two samples our hypothesis will be to assume that both the samples come from the same population ; (b) next, the actual experiment is conducted to record the observations or data and finally (c) the probability of the observed results having arisen by random sampling variation, if the null hypothesis is true, is calculated. From the calculations, the result is compared

with the standard values for different probability distribution from Statistical Tables. (The standard statistical table is the *Statistical Tables for Biological, Agricultural and Medical Research* by R. A. Fisher and F. Yates, but for general use *Cambridge Elementary Statistical Tables* by D. V. Lindley and J. C. P. Miller will serve the purpose.)

Test of significance is one of the key tools of the statisticians and now-a-days hardly any experiment is reported without subjecting the results to tests of significance in some form or other.

't' TEST—One of the simplest and often used tests of significance is known as the "t" test. The 't' test as used with small samples was worked out by "Student" (pen name of W. S. Gosset) in 1908 and modified by R. A. Fisher in 1924. The test is also referred to as "student's" t test. The 't' may be defined as a quantity representing the difference between the sample mean and the true mean or population mean expressed in terms of the standard error, viz.

$$t = \frac{(\bar{x} - \mu)}{s_{\bar{x}}}, \text{ where } \bar{x} \text{ is the sample mean, } \mu \text{ is the population mean}$$

(a hypothetical value usually regarded as 0) and $s_{\bar{x}}$ is the standard error of the sample mean.

When we want to compare two samples of small size the formula for 't' may be expressed as.

$$t = \frac{\text{difference between sample means}}{\text{standard error of the difference between means}} \\ = \frac{\bar{x}_A - \bar{x}_B}{s_d}, \text{ where } \bar{x}_A \text{ and } \bar{x}_B \text{ represent the means of the samples A and B, } s_d \text{ the standard error of the difference in means.}$$

The standard error of the difference in means (s_d) can be determined by the following formula,

$$s_d = \sqrt{\left(\frac{s_{\bar{x}_A}}{\sqrt{n_A}}\right)^2 + \left(\frac{s_{\bar{x}_B}}{\sqrt{n_B}}\right)^2}, \text{ where } s_{\bar{x}_A} \text{ and } s_{\bar{x}_B} \text{ are the standard errors of the samples A and B respectively.}$$

In order to determine whether there is any significant difference between the two samples, the value of t calculated from the formula $t = \frac{\bar{x}_A - \bar{x}_B}{s_d}$, is compared with the corresponding value for distribution of 't' at the chosen level of significance from Fisher and Yates' table (vide Appendix Table I). For this the number of degrees of freedom should be taken as $n_A + n_B - 2$. For example if there are 10 readings for each of the samples A and B, the number of degrees of freedom will be $10 + 10 - 2 = 18$. The degrees of freedom so determined is read against the column for particular probability chosen. Generally, the 5% level of significance or $P = 0.05$ is used for ordinary purposes. If the calculated value of t is found to be greater than the value from the table—then the observed difference is con-

sidered *statistically significant* and if the table value of '*t*' is lower than the calculated value the difference is *not significant*.

Another method of testing the statistical significance of the difference in means is as follows. If the difference in sample means ($\bar{x}_A - \bar{x}_B$) is greater than twice the standard error of difference of sample means (s_d), the difference in sample means is considered significant. Thus a significant difference is, when $(\bar{x}_A - \bar{x}_B) > 2s_d$.

Example 7 : Comparison of the difference between means of two samples—by '*t*' test.

Effect of two chemicals (A and B) on the height of rice seedlings—seeds of a particular variety of rice were treated with two chemicals A and B for the same period. Then these were sown separately in pots and grown under identical conditions. After 3 weeks, the height of 10 seedlings from each treatment was measured. In order to test if there is any significant difference in height between the treatments, we apply the '*t*' test.

The measurements (in cm) are tabulated and calculations are made as follows :

Treatment A			Treatment B		
Height cm	Deviation from mean $d = (x - \bar{x})$	Deviation ² d^2 or $(x - \bar{x})^2$	Height cm	Deviation from mean $d = (x - \bar{x})$	Deviation ² d^2 or $(x - \bar{x})^2$
1 22.5	-1.9	3.61	1 19.2	-2.1	4.41
2 25.6	1.2	1.44	2 24.4	3.1	9.61
3 19.8	-4.6	21.16	3 15.6	-5.7	32.49
4 26.3	1.9	3.61	4 22.8	1.5	2.25
5 22.9	-1.5	2.25	5 17.5	-3.8	14.44
6 23.4	-1.0	1.00	6 21.8	0.5	0.25
7 24.7	0.3	0.09	7 23.4	2.1	4.41
8 22.9	-1.5	2.25	8 20.2	-1.1	1.21
9 28.4	4.0	16.00	9 24.8	3.5	12.25
10 27.5	3.1	9.61	10 23.3	2.0	4.00
$n_A = 10$	$\Sigma x = 244.00$	$\Sigma d^2 = 61.02$	$n_B = 10$	$\Sigma x = 213.00$	$\Sigma d^2 = 85.32$
$\bar{x}_A = \frac{244}{10} = 24.4$			$\bar{x}_B = \frac{213}{10} = 21.3$		
$s_{\bar{x}_A} = \frac{\sqrt{\frac{\Sigma d^2}{(n-1)}}}{\sqrt{n}} = \frac{\sqrt{\frac{61.02}{9}}}{\sqrt{10}} = \frac{2.60}{3.16} = 0.823$			$s_{\bar{x}_B} = \frac{\sqrt{\frac{\Sigma d^2}{(n-1)}}}{\sqrt{n}} = \frac{\sqrt{\frac{85.32}{9}}}{\sqrt{10}} = \frac{3.08}{3.16} = 0.974$		
$t = \frac{\bar{x}_A - \bar{x}_B}{\sqrt{(s_{\bar{x}_A})^2 + (s_{\bar{x}_B})^2}}$					

Thus putting the calculated values in the above formula,

$$t = \frac{24.4 - 21.3}{\sqrt{(0.823)^2 + (0.974)^2}} = \frac{3.1}{\sqrt{1.675}} = \frac{3.1}{1.275} = 2.431$$

Comparing the calculated value of *t* with the value of *t* in the table for distribution of *t* (vide Appendix Table I) against $(n_A + n_B - 2)$ i.e. 18 degrees of freedom at $p = 0.05$, we find the latter (table value) to

be 2.101. As our calculated t i.e. 2.431 is greater than the table value we may say that the difference between the samples A and B is significant at 5% level. The chemical A has resulted in significant increase in height of rice seedlings over the chemical B.

The above formula and illustration of ' t ' test is applicable to tests involving small samples of equal size, say $n \leq 30$. But the ' t ' test may also be applied with slight modification in the formula in other cases e.g. test of paired or correlated samples of small size, comparison of sample mean with a standard : comparison of two samples of unequal size etc. For details any standard text-book on statistics may be referred to.

17.7 Correlation and Correlation Coefficient : So far we have dealt with the measurement of variation in a single variable e.g. height of plants, weight of grains or yield of crops etc. Sometimes, many important numerical investigations are concerned with the association between two different kinds of measurement or classification i.e. simultaneous variation of two variables. So that, increase or decrease in measurement (or magnitude) of one variable is related to simultaneous increase or decrease of the other variable. Thus a definite relation may exist between the variables.* In statistical terminology such relation between two or more variables is known as *correlation* and the variables exhibiting the relationship are stated to be *correlated*. For example, grain yield in rice plant may be correlated with number of tillers, so that an increase in the number of tillers will result in simultaneous increase in grain yield.

The correlation may be either *positive* or *negative*. When the variables are related in such a way that an increase in one is accompanied by an increase in the other, these are stated to be *positively correlated*. The example of grain yield and tiller number is a case of positive correlation, because the highest grain yield occurs in the plants with the highest number of tillers. On the other hand, if the increase in one variable is accompanied by a simultaneous decrease in the other variable or *vice versa*, the two variables are said to be *negatively correlated*. When no relationship can be established between the variables, these are regarded as *uncorrelated*.

For measurement of correlation the Statisticians use the *Correlation Coefficient* (r). The *correlation coefficient* may be defined as a *statistical measure of relationship between two or more variables*. The correlation coefficient may be simple, partial or multiple. But here we shall limit our discussion only to simple correlation coefficient.

The correlation coefficient (r) is expressed by the equation.

$$r = \frac{\Sigma\{(x - \bar{x})(y - \bar{y})\}}{\sqrt{\{\Sigma(x - \bar{x})^2 \cdot \Sigma(y - \bar{y})^2\}}}$$

where x and y represent the two variables ; $(x - \bar{x})$ and $(y - \bar{y})$ the deviations from the means as used in connection with the calculation of variance and standard deviation ; $\Sigma\{(x - \bar{x})(y - \bar{y})\}$ denotes the sum of the product of the deviations of x from \bar{x} and y from \bar{y} . The

above equation can be shortened down if we use the notation $d_x^{(1)}$ and d_y to denote deviation in the variables x and y respectively. Thus the equation for correlation coefficient (r) becomes :

$$r = \frac{\sum d_x \cdot d_y}{\sqrt{(\sum d_x^2 \cdot \sum d_y^2)}}$$

The correlation coefficient shall generally range between -1 and $+1$. The correlation is said to be a perfect negative one, if the $r = -1$ and if the $r = +1$ it is a case of perfect positive correlation. Values of r falling within this range are intermediate and signify varying degrees of correlation, i.e. values of r near to zero mean slight correlation and values near to $+1$ or -1 mean high correlation between the variables.

After calculating the correlation coefficient (r) we can test whether it is statistically significant or not by comparing the calculated value with the value of r from a statistical table (vide Appendix Table II), with $(n - 1)$ degrees of freedom at the desired level of probability. For example, with a calculated value of $r = 0.898$ for 9 degrees of freedom ($d.f.$), the table values of r at 0.05 and 0.01 probability (i.e. 5% and 1% levels) are 0.602 and 0.735 respectively. As the calculated value of r (0.898) exceeds the table value at both the levels, the correlation between the variables is significant and positive. Though a probability of 0.05 is considered sufficient for most of the biological experiment 0.01 or 1% level of significance signifies greater experimental precision. Here both have been shown as illustration. It is usual to signify 5% and 1% level of significance by placing one (*) or two (**) asterisks as the case may be—after the calculating value instead of writing it in words. Thus in our example $r = 0.898^{**}$.

Example 8 : Calculation of the correlation coefficient of length and weight of seeds in a variety of ground nut (*Arachis hypogea*).

The length (in centimetres) and weight (in grammes) of seeds from 10 observations are recorded and tabulated as follows :

No. of observations	Length (cm) x	Weight (gm) y	x^2	y^2	xy
1	2.2	1.1	4.84	1.21	2.42
2	2.0	0.9	4.00	0.81	1.80
3	1.6	0.8	2.56	0.64	1.28
4	1.9	0.9	3.61	0.81	1.71
5	1.7	0.7	2.89	0.49	1.19
6	2.3	1.4	5.29	1.96	3.22
7	2.0	1.0	4.00	1.00	2.00
8	2.2	1.2	4.84	1.44	2.64
9	2.4	1.2	5.76	1.44	2.88
10	2.1	1.0	4.41	1.00	2.10
$n = 10$	$\Sigma x = 20.4$	$\Sigma y = 10.2$	$\Sigma x^2 = 42.2$	$\Sigma y^2 = 10.8$	$\Sigma xy = 21.24$

After setting the tables for x and y , three other columns viz. x^2 , y^2 and xy are calculated and tabulated. Then each of the 5 columns

are totalled, these are Σx , Σy , Σx^2 , Σy^2 and Σxy . The equation for r is

$$r = \frac{\Sigma d_x d_y}{\sqrt{(\Sigma d_x^2)(\Sigma d_y^2)}}$$

Now in order to calculate the quantities $\Sigma d_x d_y$, Σd_x^2 and Σd_y^2 , short cut calculations are used to avoid lengthy arithmetic as follows :

$$\Sigma d_x d_y = \Sigma xy - \frac{(\Sigma x)(\Sigma y)}{n} \quad \text{or} \quad 21.24 - \frac{(20.4 \times 10.2)}{10} = 0.432$$

$$\Sigma d_x^2 = \Sigma x^2 - \frac{(\Sigma x)^2}{n} \quad \text{or} \quad 42.2 - \frac{(20.4)^2}{10} = 0.584$$

$$\Sigma d_y^2 = \Sigma y^2 - \frac{(\Sigma y)^2}{n} \quad \text{or} \quad 10.8 - \frac{(10.2)^2}{10} = 0.396$$

Therefore putting the above values in the equation for r , we have

$$r = \frac{0.432}{\sqrt{(0.584 \times 0.396)}} = \frac{0.432}{\sqrt{0.231}} = 0.898$$

Next, we check up the significance of the calculated value of r with the table value of r for $(n-1)$ i.e. $(10-1)$ or 9 degrees of freedom at say 0.05 level of probability (vide Appendix Table II). The value of r from the table is found to be 0.602. Thus we can say that increase in length of the groundnut seeds is correlated with the increase in weight and the correlation is positive and significant at 5% level. (The value of r calculated in the above example is significant also at 1% level).

17.8 Probability : *Probability* may be defined as *the likelihood of the occurrence of any particular form of an event* and is regarded as the ratio of the number of ways in which that form of event might occur to the total number of ways in which the event might occur in any form. If we toss a coin in the air for a number of times, we may expect to get "heads" half the times and "tails" half the time. Thus the probability of getting either a "head" or a "tail" in a single toss is 1 : 2 i. e. $\frac{1}{2}$ or 0.5. If a given trial has n possible outcomes and m of these are favourable to an event " A ", then the probability $p^{(A)}$ of getting A in a single trial is expressed as :

$$p^{(A)} = \frac{m}{n}$$

The theory of probability was developed towards the end of the eighteenth century from mathematical studies of various games of chance like drawing of cards from a pack, throwing dice, tossing of coins etc. The laws of probability may be applied to any subject involving chance or random events.

The general laws of probability are :

- (a) "the probability of simultaneous occurrence of two or more independent events is equal to the product of the probability that each will occur separately".

Example : In coin tosses, the chance of obtaining heads in any one toss is $\frac{1}{2}$, therefore the probability of obtaining 2 heads in two separate tosses is $\frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$. Thus in tossing 2 coins four times we may expect 2 heads in one of the 4 tosses. Similarly, the chance of obtaining 4 heads consecutively is $\frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1}{16}$.

Therefore with the increase in the number of tosses the probability of obtaining only heads or only tails decreases.

- (b) "the probability of the separate occurrence of either of two independent events is equal to the square root of the probability of their simultaneous occurrence—provided that the two events are of equal probability".

Example : As the probability of obtaining 2 heads from consecutive tosses is $\frac{1}{4}$, the chance of getting one head in one toss is

$$\sqrt{\frac{1}{4}} = \frac{1}{2}$$

If 4 coins are tossed in succession, the probability of any one coin falling a head or a tail is $\frac{1}{2}$; the probability of 2 coins falling heads in succession is however $\frac{1}{4}$, because, these two coins may fall in 3 other ways viz, heads and tails, tails and heads, both tails.

When a large number of coins are tossed, the total number of heads and tails obtained gives an average result. The expected result may be expressed as $(p+q)^n$, where p is the probability for getting one class (say, heads), q the probability for the other class (say, tails) and n is the number of coins tossed at a time; $p+q$ must be equal to 1. The probability for any combination of heads and tails is obtained from the expansion of the binomial $(p+q)^n$. Thus for two coin tosses $(p+q)^2 = p^2 + 2pq + q^2$, where the coefficients of the expansion represent the relative number of the times that a combination will occur, p the number of heads and q the number of tails. As p and q ($1-p$) each equals 0.5, substituting the value in the equation we have, $(0.5+0.5)^2 = (0.5)^2 + 2(0.5)(0.5) + (0.5)^2 = \frac{1}{4} + \frac{1}{2} + \frac{1}{4} = 1$. Thus out of 4 tosses 2 heads are expected once, 1 head and 1 tail twice and 2 tails once.

Where the number of individuals involved is small, the use of the binomial expansion is of great practical value in finding the probability of chance occurrence of a particular ratio among two classes of individuals. But, for problems involving more than two classes and large number of individuals other statistical methods are available. One of the methods will be discussed in the next article (17.9).

An understanding of the laws of probability is of great importance in genetics. Because it helps us in (a) forecasting the chance of obtaining certain result from a cross, (b) elucidating the operation of genetic principles, (c) assessment of "goodness of fit" of phenotypic ratio in relation to particular genetic principle. These laws can be applied to obtain the expected phenotypic ratios from multiple hybrid crosses viz. dihybrid, trihybrid etc. When only the phenotypic ratios are wanted it will be possible to avoid use of complicated checker boards by using the principles of probability. However, the actual ratios of offspring obtained from a cross very rarely exactly

tally with the expected results calculated by the principles of probability. Within certain limit this deviation between the observed and the expected result may be attributed to chance ; but when the actual results deviate to a great extent one has reason to assume that something other than chance alone is responsible. If the deviation happens 5 times out of a total of 100 cases i.e. 5% of the total cases, it may be concluded that something other than chance is involved. Several methods are available by which it can be determined when deviations from the mathematical ratio calculated by the laws of probability, are so large as to exceed the 5% limit. Chi-square (pronounced Ky-square) χ^2 test is one of the methods, which finds very wide application in problems of genetics and breeding. This method will be discussed in the next article.

17.9 Testing Goodness of fit and Chi-square Test : *When a statistical test is used to compare an "observed" ratio with an "expected" or a theoretical ratio, and to determine how closely the former fits the latter, it is known as "testing the goodness of fit".* In genetics and breeding, tests for goodness of fit are very widely used for comparison of an observed Mendelian ratio with a theoretical ratio. There are several methods for testing the goodness of fit, but the most important and popular method is the *Chi-square* (pronounced Ky-square) *Test* (χ^2). Though the Chi-square method is used by statisticians for various purposes, here we shall discuss the test in relation to testing the goodness of fit Mendelian ratios involving crosses.

CHI-SQUARE TEST : It may be defined as a *statistical comparison of observed ratios with theoretical ratios*. The measure of deviation of the ratios is denoted by χ^2 (chi-square) and calculated from the equation :

$$\chi^2 = \sum \frac{(O - E)^2}{E} \text{ where } O = \text{the observed number or frequency,}$$

E = the number or frequency expected on the basis of theoretical consideration and \sum is the symbol denoting summation.

When a breeding experiment is conducted and observations are recorded, the progenies segregate in certain ratios. The theoretical ratio likely to be obtained according to Mendelian principles is also known to us. But since the chance factor is there and we test only a small sample of the population, it is highly unlikely that the observed and expected (theoretical) ratios will be in total agreement. In order to test the "goodness of fit" of the observed results, it is necessary to find, (i) the *deviation* between the observed and the expected results and (ii) the *probability value* corresponding to the deviation. Considering the variability in biological materials, a probability of 0.05 is taken as significant, which means that the event (in this case the deviation) is not likely to occur more than 5 times out of 100 tests. Let us try to understand the method of calculating χ^2 with the help of examples from Mendel's experiments with garden peas.

Example 9 : Testing the "goodness of fit" of monohybrid ratio by χ^2 method.

Some plants of a *tall* variety of garden pea were crossed with a *dwarf* variety. The resulting F_1 plants were all tall. These were carefully selfed. The F_2 generation thus obtained was found to consist of 787 tall plants and 277 dwarf plants, out of a total of 1064 plants. According to Mendel's principles the phenotypic segregation of a monohybrid cross in F_2 should be in the ratio of 3 : 1 (tall : dwarf). Now we shall test how the observed data fits with the expected data. The data are arranged in a tabular form and calculations are done as follows :

Classes	Tall	Dwarf	Total
Observed Numbers (O)	787	277	1064
Expected Numbers (E)	798	266	1064
Deviation ($O - E$)	-11	+11	0
$(O - E)^2$	121	121	
$\frac{(O - E)^2}{E}$	$\frac{121}{798}$	$\frac{121}{266}$	
	=0.1516	=0.4541	

$$\therefore \chi^2 = \sum \frac{(O - E)^2}{E} = 0.1516 + 0.4541 = 0.6057$$

After the value of χ^2 has been calculated, it is compared with the table for distribution of χ^2 in statistical tables (vide Appendix Table III). The table of χ^2 gives the values of χ^2 at different levels of probability, which may be obtained only when the deviations between the observed and the expected ratios are random. But before we consult the table of χ^2 , it is necessary to know the number of degrees of freedom, because in the statistical table for the distribution of χ^2 each row relates to a given number of degrees of freedom. In general if there are n classes in the table set up for calculating χ^2 , there should be $(n - 1)$ degrees of freedom. Thus in our example, there are 2 classes i.e. *tall* and *dwarf*, so that there will be $(2 - 1)$ or 1 *d.f.* With three classes there will be 2 *d.f.*, with 4 classes 3 *d.f.* and so on. Now, in the example with 1 *d.f.* the calculated value of χ^2 (0.6057), the probability lies between 0.50 and 0.30. As this is a high probability value, there is a *good fit* between the observed and the expected ratios. So, in our example Mendel's principle is supported by the data. It should be noted, however, that the probability values vary according to χ^2 and *d.f.* ; the higher the value of χ^2 , the lower is the probability that the observed data fit the expected ones based on the theory. In general, to be a good fit the calculated value of χ^2 should be *lower* than the table value of χ^2 at 0.05 probability.

Example 10 : Testing the "goodness of fit" of dihybrid ratio by χ^2 method.

A variety of garden pea with round and yellow seed (YYRR) characters was crossed with another variety having the characters

wrinkled and green (yyrr). The F_1 offsprings were all yellow round. These were selfed and the resulting progeny in the F_2 was found to consist of 4 types of seeds as follows : 315 round and yellow, 101 wrinkled and yellow, 108 round and green, 32 wrinkled and green. According to Mendel's principles the F_2 in a dihybrid cross segregates in the ratio of 9 : 3 : 3 : 1. We can now check how the observed result fits with the hypothetical ratio.

Classes	Round yellow	Wrinkled yellow	Round green	Wrinkled green	Total
Observed Numbers (O)	315	101	108	32	556
Expected Numbers (E)	312.75	104.25	104.25	34.75	556
Deviation (O - E)	+2.25	-3.25	+3.25	-2.25	0
(O - E) ²	5.0625	10.56	10.56	5.0625	
$\frac{(O - E)^2}{E}$	$\frac{5.0625}{312.75}$	$\frac{10.56}{104.25}$	$\frac{10.56}{104.25}$	$\frac{5.0625}{34.75}$	
	= 0.01612	= 0.1013	= 0.1013	= 0.1457	

$$\chi^2 = \sum \frac{(O - E)^2}{E} = 0.01612 + 0.1013 + 0.1013 + 0.1457$$

$$= 0.3645$$

Comparing the calculated value of χ^2 with the table for distribution of χ^2 (Appendix Table III), for 3 degrees of freedom (4 classes - 1), we find that the value lies between p 0.95 and 0.90. This is a very high value and thus the observed result fits the expected result very very well. This is an example of a rather extreme case of goodness of fit.

Though the chi-square test is a very useful one for measuring the goodness of fit and is in wide use, there are certain restrictions against its use in genetics and breeding. The first is that the χ^2 test can generally be applied only to numerical frequencies and not to percentages or ratios obtained from them, secondly, the test is reliable only when the observed or the expected frequency in any class is 5 or more. In other words, the χ^2 test can not be properly used in cases where the frequency in any class is less than five.

In working out the problems in Biometry, a lot of calculations are involved. It is most convenient to work with a calculating machine, but when a machine is not available, much of the medium of arithmetical calculations is eased by the use of "*Barlow's Tables of Square. Cubes, Square Roots, Cube Roots and Reciprocals*" — edited by L. J. Comrie, 4th edition, 1941, published by E. & F. N. Spon Ltd. London.

APPENDIX TABLE I. DISTRIBUTION OF t
Probability, p

Degrees of freedom (n)	.2	.1	.05	.02	.01	.001
1	3.078	6.314	12.706	31.821	63.657	636.619
2	1.886	2.920	4.303	6.965	9.925	31.598
3	1.638	2.353	3.182	4.541	5.841	12.924
4	1.533	2.132	2.776	3.747	4.604	8.610
5	1.476	2.015	2.571	3.365	4.032	6.869
6	1.440	1.943	2.447	3.143	3.707	5.959
7	1.415	1.895	2.365	2.998	3.499	5.408
8	1.397	1.860	2.306	2.896	3.355	5.041
9	1.383	1.833	2.262	2.821	3.250	4.781
10	1.372	1.812	2.228	2.764	3.169	4.587
11	1.363	1.796	2.201	2.718	3.106	4.437
12	1.356	1.782	2.179	2.681	3.055	4.318
13	1.350	1.771	2.160	2.650	3.012	4.221
14	1.345	1.761	2.145	2.624	2.977	4.140
15	1.341	1.753	2.131	2.602	2.947	4.073
16	1.337	1.746	2.120	2.583	2.921	4.015
17	1.333	1.740	2.110	2.567	2.898	3.965
18	1.330	1.734	2.101	2.552	2.878	3.922
19	1.328	1.729	2.093	2.539	2.861	3.883
20	1.325	1.725	2.086	2.528	2.845	3.850
21	1.323	1.721	2.080	2.518	2.831	3.819
22	1.321	1.717	2.074	2.508	2.819	3.792
23	1.319	1.714	2.069	2.500	2.807	3.767
24	1.318	1.711	2.064	2.492	2.797	3.745
25	1.316	1.708	2.060	2.485	2.787	3.725
26	1.315	1.706	2.056	2.479	2.779	3.707
27	1.314	1.703	2.052	2.473	2.771	3.690
28	1.313	1.701	2.048	2.467	2.763	3.674
29	1.311	1.699	2.045	2.462	2.756	3.659
30	1.310	1.697	2.042	2.457	2.750	3.646
40	1.303	1.684	2.021	2.423	2.704	3.551
60	1.296	1.671	2.000	2.390	2.660	3.460
120	1.289	1.658	1.980	2.358	2.617	3.373
∞	1.282	1.645	1.960	2.326	2.576	3.291

Appendix Table I is abridged from Table III of Fisher & Yates : *Statistical Tables for Biological, Agricultural and Medical Research*, published by Oliver & Boyd, Edinburgh, and by permission of the authors and publishers.

APPENDIX TABLE II

VALUE OF THE CORRELATION COEFFICIENT (r) FOR DIFFERENT
LEVELS OF SIGNIFICANCE

Degrees of freedom (n)	.1	.05	.02	.01	.001
1	.98769	.99692	.999507	.999877	.9999988
2	.90000	.95000	.98000	.990000	.99900
3	.8054	.8783	.93433	.95873	.99116
4	.7293	.8114	.8822	.91720	.97406
5	.6694	.7545	.8329	.8745	.95074
6	.6215	.7067	.7887	.8343	.92493
7	.5822	.6664	.7498	.7977	.8982
8	.5494	.6319	.7155	.7646	.8721
9	.5214	.6021	.6851	.7348	.8471
10	.4973	.5760	.6581	.7079	.8233
11	.4762	.5529	.6339	.6835	.8010
12	.4575	.5324	.6120	.6614	.7800
13	.4409	.5139	.5923	.6411	.7603
14	.4259	.4973	.5742	.6226	.7420
15	.4124	.4821	.5577	.6055	.7246
16	.4000	.4683	.5425	.5897	.7084
17	.3887	.4555	.5285	.5751	.6932
18	.3783	.4438	.5155	.5614	.6787
19	.3687	.4329	.5034	.5487	.6652
20	.3598	.4227	.4921	.5368	.6524
25	.3233	.3809	.4451	.4869	.5974
30	.2960	.3494	.4093	.4487	.5541
35	.2746	.3246	.3810	.4182	.5189
40	.2573	.3044	.3578	.3932	.4896
45	.2428	.2875	.3384	.3721	.4648
50	.2306	.2732	.3218	.3541	.4433
60	.2108	.2500	.2948	.3248	.4078
70	.1954	.2319	.2737	.3017	.3799
80	.1829	.2172	.2565	.2830	.3568
90	.1726	.2050	.2422	.2673	.3375
100	.1638	.1946	.2301	.2540	.3211

Appendix Table II is abridged from Table VII of Fisher & Yates : *Statistical Tables for Biological, Agricultural and Medical Research*, published by Oliver & Boyd, Edinburgh, and by permission of the authors and publishers.

APPENDIX TABLE III. DISTRIBUTION OF χ^2
Probability, p

Degrees of freedom (n)	.99	.98	.95	.90	.80	.50	.20	.10	.05	.02	.01	.001
1	.03157	.03628	.00393	.0158	.0642	.455	1.642	2.706	3.841	5.412	6.635	10.827
2	.0201	.0404	.103	.211	.446	1.386	3.219	4.605	5.991	7.824	9.210	13.815
3	.115	.185	.332	.584	1.005	2.366	4.642	6.251	7.815	9.837	11.345	16.266
4	.297	.429	.711	1.064	1.649	3.357	5.989	7.779	9.488	11.668	13.277	18.467
5	.554	.752	1.145	1.610	2.343	4.351	7.289	9.236	11.070	13.388	15.086	20.515
6	.872	1.134	1.635	2.204	3.070	5.348	8.558	10.645	12.592	15.033	16.812	22.457
7	1.239	1.564	2.167	2.833	3.822	6.346	9.803	12.017	14.067	16.622	18.475	24.322
8	1.646	2.023	2.733	3.490	4.594	7.344	11.030	13.362	15.507	18.168	20.090	26.125
9	2.088	2.532	3.325	4.168	5.380	8.343	12.242	14.684	16.919	19.679	21.666	27.877
10	2.558	3.059	3.940	4.865	6.179	9.342	13.442	15.987	18.307	21.161	23.209	29.588
11	3.051	3.609	4.575	5.578	6.989	10.341	14.631	17.275	19.675	22.618	24.725	31.264
12	3.571	4.178	5.226	6.304	7.807	11.340	15.812	18.549	21.026	24.054	26.217	32.909
13	4.107	4.765	5.892	7.042	8.634	12.340	16.985	19.812	22.362	25.472	27.688	34.528
14	4.660	5.368	6.571	7.790	9.467	13.339	18.151	21.064	23.685	26.873	29.141	36.123
15	5.229	5.985	7.261	8.547	10.307	14.339	19.311	22.307	24.996	28.259	30.578	37.697
16	5.812	6.614	7.962	9.312	11.152	15.338	20.465	23.542	26.296	29.633	32.000	39.252
17	6.408	7.255	8.672	10.085	12.002	16.338	21.615	24.769	27.587	30.995	33.409	40.790
18	7.015	7.906	9.390	10.865	12.857	17.338	22.760	25.983	28.869	32.346	34.805	42.312
19	7.633	8.567	10.117	11.651	13.716	18.338	23.900	27.204	30.144	33.687	36.191	43.823
20	8.260	9.237	10.851	12.443	14.578	19.337	25.038	28.412	31.410	35.020	37.566	45.315
21	8.897	9.915	11.591	13.240	15.445	20.337	26.171	29.615	32.671	36.343	38.932	46.797
22	9.542	10.600	12.338	14.041	16.314	21.337	27.301	30.813	33.924	37.659	40.289	48.268
23	10.196	11.292	13.091	14.848	17.187	22.337	28.429	32.007	35.172	38.968	41.638	49.728
24	10.856	11.992	13.848	15.659	18.062	23.337	29.553	33.196	36.415	40.270	42.980	51.179
25	11.524	12.697	14.611	16.473	18.940	24.337	30.673	34.382	37.652	41.566	44.314	52.620
26	12.198	13.409	15.379	17.292	19.820	25.336	31.795	35.563	38.885	42.856	45.642	54.052
27	12.879	14.125	16.151	18.114	20.703	26.336	32.912	36.741	40.113	44.140	46.963	55.476
28	13.565	14.847	16.928	18.939	21.588	27.336	34.027	37.916	41.337	45.419	48.278	56.893
29	14.256	15.574	17.708	19.768	22.475	28.336	35.139	39.087	42.557	46.693	49.588	58.302
30	14.953	16.306	18.493	20.599	23.364	29.336	36.250	40.256	43.773	47.962	50.892	59.703

Appendix Table III is abridged from Table IV of Fisher & Yates: *Statistical Tables for Biological, Agricultural and Medical Research*, published by Oliver & Boyd, Edinburgh, and by permission of the authors and publishers.

SELECTED QUESTIONS

1. What is the modern concept of a plant cell ? Describe the different sub-cellular structures in a plant cell.

Refer article 1.1 and article 3.2 (in *plant physiology* portion)

2. Give a concise account, with suitable diagrams, of the changes the nucleus undergoes during the division of a vegetative cell.

Refer article 2.1

3. What is meiosis ? Describe the process in detail with suitable sketches. What is its significance in the life history of a plant ?

Refer article 2.2

4. Represent diagrammatically the various stages of meiosis and point out the distinctive features of this process.

Refer figure 2.3 and 2.4 and article 2.2

5. Give an account of the process of meiosis in detail and the significance of this process in the life cycle of the plant.

Refer article 2.2 and *significance of meiosis* under same article

6. What are the essential points of differences between a division by mitosis from that of a meiosis. Illustrate your answer with diagrams assuming the chromosome number to be $2n=4$.

Refer article 2.3

7. Describe the morphology of chromosomes. Mention the important constituents of a chromosome.

Refer article 3.1

8. Describe the morphology of chromosomes. Give in detail the chemical nature of chromosomes.

Refer articles 3.1 and 3.3

9. Describe the morphology of a typical chromosome. Explain the difference between karyotype and idiogram and indicate the importance of karyotype analysis in plants.

For first part refer article 3.1. Then add :

The general morphology of a set of chromosomes at the metaphase stage of an individual or species is known as *karyotype*. It deals mainly with the comparative size, shape and morphology of the different chromosomes. A diagrammatic representation of the chromosomes of an individual showing all the morphological features of the chromosomes, is known as *idiogram*. All possible details of the chromosomes including, their dimensions, position of the centromere and the presence of the secondary constrictions and satellite bodies can be studied by karyotypic analysis.

10. Write functions of (a) Centromere, (b) Secondary constriction, (c) DNA, (d) Mitochondria.

For (a) refer article 3.1

(b) refer article 3.1

(c) refer article 3.3

(d) refer article 3.2B (*plant physiology* portion)

11. Differentiate clearly between chromosome, chromonema and chromatid. When does a chromosome divide in mitosis and meiosis ? Give an outline of the prophase of meiosis with suitable drawings.

For first part refer article 3.1. Then add the *introduction* of chapter 2.
For last part refer article 2.2

12. What are the chief chemical constituents of chromosome. Give a precise answer with reasons.
Refer article 3.3
13. Describe the structure of a 'salivary gland' and lampbrush chromosome with diagrams.
Refer article 3.2
14. What is translocation ? How does it differ from inversion ? Give a short account of the meiotic behaviour of a translocation and inversion heterozygotes. How many types of progeny are expected from the former ?
Refer chapter 4, article 4.1 and 4.2
15. What are polyploids ? How are they classified ? Briefly outline their role in evolution with special reference to crop plants.
Refer *introduction* of chapter 5 and *importance of polyploidy* in article 5.1
16. What do you mean by '2n' number of chromosomes in plants ? Can this number be changed ? If so, how ?
Refer chapter 5
17. What is polyploidy ? Briefly indicate the method by which polyploidy can be induced. What is the importance of polyploidy in the improvement of crop plants ?
Refer *introduction* of chapter 5 and *induction of polyploidy and importance of polyploidy* in article 5.1
18. What are the autopolyploid ? How do they differ from the diploids and amphidiploids ?
Refer article 5.1
19. Describe a method adopted for the induction of polyploidy in a plant. Explain the economic importance of such induced polyploid plants.
Refer *induction of polyploid and importance of polyploids* in article 5.1. Colchicine (obtained from the roots and corm of *Colchicum autumnale* (Liliaceae) is the most effective for inducing polyploidy. Colchicine may be applied either in aqueous solution or in liquid form in agar solution or making a paste with lanoline. These are applied in cut stems or growing buds. Colchicine, when applied to seeds and seedlings, produced tetraploid plants.
20. What is a "gene" ? How it acts ? Describe its chemical nature.
Refer *introduction* of chapter 6 and articles 6.1 and 6.2
21. State the First and Second Laws of Mendel. Describe the experiments carried out by Mendel and explain the results.
Refer articles 7.1 and 7.2
22. Explain with suitable examples the laws of "Purity of gametes" and "Independent assortment of genes" as enunciated by Mendel.
Refer chapter 7, articles 7.1 and 7.2
The law of segregation is also called law of the 'purity of gametes' as the gametes for tallness or dwarfness are pure.
23. Explain Mendel's Laws of inheritance.
Refer chapter 7
24. Give a short account of Mendel's experiments on the inheritance of characters in plants and state the laws.
Refer articles 7.1 and 7.2

25. What is the Mendelism? Justify the statement—"Mendel was fortunate in selecting sweet pea as his experimental material."
Refer chapter 7. For the last part of the question refer the *Introduction* of chapter 7.
26. Describe briefly Mendel's Laws of inheritance and explain its importance in genetical studies.
Refer chapter 7
27. Give a short account of Mendel's experiments on inheritance of characters. State the laws deduced from them and call attention to such modifications to the laws which become imperative during the present century.
Refer articles 7.1, 7.2 and 7.3
28. Mention those cases which show that Mendel's laws are not absolutely correct.
Refer article 7.4
29. What is meant by multiple factor inheritance? Two white-flowered strains of sweet peas while crossed gave purple flowers in the F_1 progeny. On selfing F_2 ratio was 9 purple: 7 white. Explain the mode of inheritance and genotypes involved with aid of a checkerboard.
Refer *introduction* of chapter 8 and article 8.5
30. What are the evidences that show that genes often do not behave independently but maintain a relationship with the neighbouring genes?
Refer chapter 8
31. What kind of factor interaction is indicated when the 9 : 3 : 3 : 1 ratio is modified to 9 : 3 : 4? Illustrate your answer by a suitable example and checkerboard.
Refer article 8.6
32. In rice dominant genes—purple leaf (L_p) and green leaf (I) interact to modify the F_2 ratio into 13 : 3. Elucidate the phenomenon.
Refer article 8.7
33. When two white-flowered sweet pea plants were crossed, the F_1 flower colour was purple and on selfing the F_2 plants segregated into purple-flowered and white-flowered types only. Elucidate the phenomenon.
Refer article 8.5
34. Explain the phenomenon of linkage and mention its significance in the inheritance of characters.
Refer article 9.1 (omit *detection of linkage*)
35. Explain linkage and crossing over.
Refer articles 9.1 and 9.2
36. "Crossing over is an exception to linkage and is due to the exchange of parts between homologous chromosome"—Explain the statement.
Refer article 9.2
37. Define mutation and briefly discuss the importance of the phenomenon in evolution.
Refer *introduction* of chapter 10 and *importance of polyploidy* under article 5.1
38. Define mutation. Explain and classify the different types of mutations with suitable examples.
Refer chapter 10

39. How can you detect a point and a chromosomal mutation. Give an account of the different types of chromosomal mutation occurring in nature.
Refer chapter 10 and for 'chromosomal mutation' refer chapter 4 and 5
40. Certain characters are mostly associated with sex—why ? Mention at least one such case.
Refer article 11.2
41. How has it been proved experimentally that cytological crossing over is associated with genetic recombination of characters ?
Refer *cytological basis of crossing over* in article 9.2
42. What is crossing over ? When and how does it occur ? Give a detailed account of the prophase stage of meiosis.
Refer first part of article 9.2 and *mechanism of crossing over* in the same article. For the last part refer article 2.2
43. What are sex chromosomes ? Give an account of the different methods of the determination of sex in plants.
Refer articles 11.1 and chapter 12
44. In reciprocal crosses results often differ—why ?
Refer chapter 13
45. In most animals a large amount of cytoplasm is carried by the egg than by the sperm. Likewise the egg in plants carries more cytoplasm than the pollen. How could this difference affect the expression of inherited traits ?
Refer chapter 13
46. Reciprocal crosses sometimes give different results in the F_1 . This may be due to (a) sex-linked inheritance, (b) cytoplasmic inheritance or (c) maternal effects. If such a result was obtained how could the investigator determine experimentally which category was involved ?
Refer chapter 11 (article 11.2) and chapter 13
47. What are the objectives of plant breeding ? Describe an important method of plant breeding and state the precautions that should be taken in the procedure.
Refer chapter 14 and 15
48. List the different steps involved in hybridization procedure of a new variety. Give a brief account of each step.
Refer chapter 15 and article 15.2
49. What are the different hybridization methods for self and cross pollinated crops ?
Refer chapter 15 article 15.3
50. Define the term "pure line". How the pure line selection is applied in improving crop plants.
Refer chapter 15 and article 15.2 (under *Selection*)
51. How many steps are involved in the hybridization procedure ? Describe them in detail.
Refer chapter 15 and article 15.2
52. What is heterosis ? What genetical theories have been put forth to explain the cause of heterosis ?
Refer chapter 16 and article 16.1
53. What do you mean by "plant introduction and acclimatization" ? What steps are involved in the procedure of plant introduction.
Refer chapter 15 and article 15.2(1)

54. Write notes on ;

- (i) Heterochromation—Refer article 1'4
- (ii) Emasculation—Refer article 15.2
- (iii) Inversions—Refer chapter 4, article 4.2
- (iv) Back cross—Refer *detection of linkage* in article 9.1
- (v) Plastid inheritance—Refer article 13.2
- (vi) Polyploidy—Refer article 5.1
- (vii) Mendelian segregation—Refer chapter 7 article 7.1
- (viii) Crossing over—Refer article 9.2
- (ix) Mutagen—Refer *induced mutation* in chapter 10
- (x) Allelomorph—Refer *introduction* of chapter 7
- (xi) Dihybrid ratio—Refer article 7.2
- (xii) Sex-chromosomes—Refer article 11.1
- (xiii) Linkage—Refer article 9.1
- (xiv) DNA—Refer article 3.3
- (xv) Genotype and phenotype—Refer article 7.1
- (xvi) Test cross—Refer *detection of linkage* in article 9.1
- (xvii) Amphidiploidy—Refer article 5.1
- (xviii) Deletions—Refer article 4.1
- (xix) Incomplete dominance—Refer article 8.1
- (xx) Goodness of fit—Refer article 17.9
- (xxi) *Raphanobrassica*—Refer *importance of polyploidy* in article 5.1
- (xxii) Lethal gene—Refer article 8.2
- (xxiii) Chi-square—Refer article 17.9
- (xxiv) Plectonemic and Paranemic coiling—Refer article 2.5
- (xxv) Terminalization—Refer *diplotene stage* in article 2.1
- (xxvi) B-chromosome— Refer article 3.2(3)
- (xxvii) Nullisomic—Refer article 5.2
- (xxviii) Gene action—Refer article 6.2
- (xxix) Tautomeric shift—Refer *Basis of mutation* in chapter 10
- (xxx) Homogametic sex—Refer article 11.1
- (xxxi) Sex-linked inheritance—Refer article 11.2
- (xxxii) Criss cross inheritance—Refer article 11.2
- (xxxiii) Homologous chromosomes—Refer *Zygotene stage* in article 2.1
- (xxxiv) Bivalents—Refer *Zygotene stage* in article 2.1
- (xxxv) Chiasma—Refer *Diplotene stage* in article 2.1
- (xxxvi) Genome—Refer article 3.1
- (xxxvii) Salivary gland chromosome—Refer article 3.2(1)
- (xxxviii) Chromonemata—Refer article 3.1
- (xxxix) mRNA—Refer article 3.3
- (xxxx) Position effect—Refer *inversion* in article 4.2

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EVOLUTION

1.1 Ideas and Definition of Evolution : Evolution is the theory according to which complex forms are considered to have been derived from simpler ones. The word 'evolution' has been derived from the Latin word '*evolvere*' which means to *unroll* or *unfold* i.e. the development of something by slow natural processes from rudimentary to more highly organised condition.

Evolution, therefore, may be defined as the gradual and slow development or change of something by natural processes—this change may include the change or development of something like the origin and evolution of the earth ; of the land masses on the earth ; of seas, mountains etc. ; of the living organisms like plants and animals on the earth etc. The last type i.e. the evolution of living organisms e.g. plants and animals comes under the *organic evolution*.

So, organic evolution means the origin and appearance of new living organisms (both plants and animals) on the earth as a result of slow and steady natural processes of continuous change. The term organic evolution may also be defined more precisely as "*cumulative change in the characteristics of organisms, occurring in successive generations related by descent*"¹ or "*as the organisation of species of animals and plants as conceived by those who attribute it to a process of development from earlier forms and not as a process of special creation*"² or "*as the doctrine according to which higher forms of life have gradually arisen out of lower*"³. Charles Darwin (1859) has defined evolution simply as "*descent with modification*".

Regarding the mode of evolution, there are two main trends e.g. (a) *progressive evolution* i.e. the upward direction of the evolution, which takes place gradually from simple predecessors to complex types resulting thereby in more complexity and elaboration in structure, and (b) *regressive or retrogressive evolution* i.e. the downward direction of the evolution, where evolution takes place from complex to simpler types due to reduction and suppression of organs resulting thereby in decline or degeneration in structure.

It is now assumed that present living organisms, both plants and animals have evolved as a result of modifications and changes from simplest types of existing forms. The derivation or origin of different and diverse types of organisms did not take place in a year or two but gradually through the ages comprising millions of years. No form of life either plant or animal existed in the earth during the first phase

¹ Dictionary of Biology

² Oxford Dictionary, ³ Chambers's Twentieth Century Dictionary

of creation of the earth for several hundreds of millions of years. The earth itself evolved out of gaseous burning mass which gradually cooled down; consequently its surface solidified giving rise to lands, oceans and atmosphere. The origin of life began in water in an exceedingly simple form as a minute protoplasmic speck from disintegrated inorganic matters owing to chemical and physical changes which were accidental and whim of nature. This simplest living being could carry on all life processes *e.g.* growth, reproduction and other metabolic activities. At the time of appearance of the simplest first living being, there was no difference between plants and animals. These simple life-forms passed through millions of generations without appreciable change, until with the change of earth's condition—this slowly gave rise to variations and modification which were better adapted to newer conditions. The two phenomena of *variation* and *adaptation* are the prime factors in causing evolution of new forms of life. Evolution of life then took place into two phyla (a) in the development of animals and (b) in the development of plants. Plant and animal-forms underwent repeated changes as a consequence of adaptation and environments.

Life in the form of simplest organisms came into existence first. From such simplest organisms higher orders of plants and animals gradually evolved. No organisms evolved *de novo*. The modifications and changes of simpler organisms (like viruses and bacteria) leading to the origin of higher forms gradually took place through ages comprising millions of years or so. Whatever the origin of viruses and bacteria may have been, the different divisions of algae have evolved from bacterial ancestors, probably from the members of autotrophic bacteria. But it is not clearly understood from any available evidence whether the different algal divisions arose independently or from a common stock. The blue green algae (Cyanophyta) are the earliest plants known from the fossil record—they are extraordinarily primitive in their lack of a distinct nucleus or plastids but they contain chlorophyll. From this fact it is easily understandable that the Cyanophyta may be ancestral to some other algal divisions including Chlorophyta, although the actual evidence of this concept is still meagre. The origin of two groups of moulds *viz.* Myxomycophyta and Eumycophyta is also doubtful, their origin may be from bacterial ancestor, or from algae due to loss of chlorophyll, or even from Protozoa. However much controversial the problem of the origin of those lower groups of plants may be, it appears clearly that the land plants with two major divisions *e.g.* Bryophyta and Tracheophyta (vascular plants) arose from the green algae independently. The bryophytes further have become differentiated into three major groups *viz.* liverworts, hornworts and mosses, but these groups have not produced further any progressive types of plants. The earliest and primitive tracheophytes (*i.e.* psilophytes of Pteridophyta) have succeeded in colonising the land. This division quickly gave rise to three major sub-divisions *viz.* the Lycopsidea (Lepidophyta), the Sphenopsida (Calamophyta) and the

Pteropsida (Pterophyta). For the time being, the first two were dominant groups, but were reduced to minor groups at the end of Paleozoic Era. At first the pteropsid line was represented by the ferns only, but this line ultimately gave rise to the gymnosperms which in turn seem to have given rise to the angiosperms. From the more primitive sub-class of angiosperms *i.e.* dicots, much more specialised sub-class monocots has arisen in course of time.

But great problem arose in ascertaining how, when and under what conditions did all these living organisms come into existence. Various theories, since the time of Greek philosophers, have been put forward to explain the origin of living organisms—these are :

(1) *Theory of Eternity*—The ancient people believed that all the varied forms of the present-day plants and animals have been there from the beginning of the earth and they will continue to live for ever without any change till eternity.

(2) *Theory of Special Creation*—According to this idea, each and every life-form was created by some supernatural power as a separate and fixed entity. Each life-form was unable to change itself or to give rise to other types of life-forms and was therefore not related by descent to any other. This view was first advocated by a Spanish priest Suarez (1548—1677). According to him “everything was made in six days.” On the first day, earth was made; on the third day, ancestors of plants and animals suddenly appeared; on the fifth and sixth days, ancestors of all present-day living beings appeared. Theory of special creation was believed previously by many faithful and religious minded people of the West for many centuries although idea of this theory still persists in the minds of modern people.

(3) *Theory of Catastrophism*—This theory was proposed by a French palaeontologist Cuvier (1769—1832) from the discovery and study of fossils. It was discovered that all the plants and animals lived in a particular area of the earth for a definite period, after which again a fresh lot of living organisms reappeared. It was also studied that plants and animals which lived in a particular period were different from those of earlier or later periods. This theory explained the above conditions on the basis of the fact that “the earth was visited periodically by catastrophics which destroyed all life-forms, time to time, each catastrophe being followed by new and specially created forms of life.”

(4) *Theory of Spontaneous Origin or Theory of Abiogenesis*—Some believed that various types of living organisms originated spontaneously from non-living substances (like mud, rocks, remains of plants and animals, decaying matters etc.) automatically in course of time. Thus Aristotle believed that mosquitos and fleas arose from decaying matter. Tadpoles, worms and many other micro-organisms were supposed to arise from mud. Flies were supposed to be formed from putrefying flesh. This theory has been discarded by many

scientists like Redi (an Italian physician), Spallanzani (Italian priest) and others on the basis of the fact that life can not be formed *de novo*, instead life must come from some pre-existing one e. g. formation of new bacteria and fungi due to the multiplication of pre-existing bacteria and spores of fungi.

(5) *Theory of Organic Evolution or The Doctrine of Descent*—This is the most modern concept of the evolution. According to this theory, the plants and animals that have inhabited the earth have been changing through millions of years in the different geological periods of the earth's history. This change is very slow, gradual and in orderly form, as a result of this type of change more complex and varied forms of plants and animals have been derived from the simpler types that existed in the beginning of the earth. This theory was first put forward by earlier Greek philosophers like Democritus, Aristotle and others. But the real proof of the organic evolution came from the contribution of later workers like Linnaeus (1707-1778), Buffon (1702-1788), Erasmus Darwin (1731-1802), Lamarck (1744-1829), St.-Hilaire (1772-1844), Charles Darwin (1809-1882), Weisemann (1834-1914), Hugo de Vries (1848-1935) and others.

CHAPTER 2

Evidences of Organic Evolution

Now-a-days all biologists believe in the theory of organic evolution that has occurred among plants and animals. Now controversy arises as to how evolution i. e. gradual changes took place. To answer this question, the various facts and evidences in favour of the organic evolution are briefly discussed below :—

(1) *Taxonomic Evidence* i. e. *Evidence from Classification*—The modern systems of classification are based on phylogeny, which bear strong testimony that many related groups of plants and animals were derived from common ancestors. Most of the phylogenetic systems of classification have endeavoured to establish genetic and ancestral relations ; so the present forms of plant-life are the product of evolutionary process. In this world there are numerous kinds of plants, some of which bear close resemblances, some do not ; again some groups of plants have simple structure while some are complex. The former, according to the modern phylogenetic classification, were evolved first and have priority of being placed in the first and treated as early group. A concrete example explains this, the Ranales is the first order of the dicots that had the earliest origin and consequently placed first in order of priority in the classification. whereas the Tubiflorae and Campanulatae are the orders which are of recent origin and placed last. In the modern scientific classification the orders are arranged and classified according to their link of relationships and evolution from others e. g. the Malvales, Rosales etc. have originated from the Ranales from different lines and consequently arranged in order of the priority of evolution. So the taxonomic arrangements of orders bear testimony to evolution of plants in different lines from common ancestor. The common ancestor of the Ranales was probably Bennettitales or any other hypothetical pro-angiosperm whatever may be, the evidence of which has been obtained from the comparative study of fossils.

(2) *Geological Evidence* or *Evidence from Fossils*—Fossils are the petrified remains or the impressions of ancient plants and animals. Fossils furnish sound evidence regarding the existence of plants and animals that lived on this earth in different geological periods. According to the theory organic evolution, the present-day plants and animals have descended from the simplest types of life of the past by the gradual increase in the complexity of life. Fossil records from different geological periods, though incomplete, show some continuous and unbroken series of intermediate forms between the past and the present forms. The earth's surface is composed of different layers or strata of rocks formed in different ages. These

different strata of rocks were found to bear fossils of different types of plants and animals. The first formed rocks are called *Archeozoic rocks* which did not contain any living organism—next formed rocks are called *Proterozoic* in which little evidence of life was noted. Next, gradually *Paleozoic rocks* and *Mesozoic rocks* were formed—in these era different forms of plant and animal life were originated. The rocks Mesozoic to the present day are called *Cenozoic*—in this strata living organisms of recent forms are seen. The study of fossils greatly helps in tracing the evolution of some plants and animals. Fossils, though, show sometimes wide gaps in the evolutionary history of plants and animals, still help in tracing connecting links between the past and the present forms of living organisms. As for example, the pteridosperms or seed ferns—this group of plants shows the mixed characters of pteridophyta and gymnosperms—hence form a transitional group between pteridophyta and cycad-like gymnosperms. Again, the *Calamites* (a fossil pteridophyta) of the Carboniferous age show great similarities with our present-day members of Equisitales. The tall *Cordaites* of the past resemble modern Liliaceous tree *Yucca* (angiosperm), again the leaves of fossil *Ginkgo* resemble the leaves of present-day *Ginkgo biloba*. All these examples indicate that the evolution took place in a direct line from ancient types to present-day types.

(3) *Morphological and Anatomical Evidences*—The study of comparative morphology and anatomy strongly supports the theory of evolution. Many different types of plants show their structural similarities of different organs like stems, roots, leaves, flowers etc. and other morphological characters among different groups of plants e.g. the similar structure of archegonia in bryophytes, pteridophytes and gymnosperms. The similarity in the structure of the strobili of some pteridophytes (Lycopods) and gymnosperms etc. prove that the latter might have evolved from the former. Similarly presence of vestigial carpels (pistilodes) and stamens (staminodes) in many members of angiosperm families supports that the origin of dicliny in flowers had taken place from hermaphrodite ancestors as a result of reduction in course of time. Sometimes reversion to the original characters in the development of hermaphrodite flowers in some plants having unisexual flowers is also noted. Morphological similarities among the plants of the same group in the form of calyx and corolla, cohesion and adhesion of stamens and carpels, type of leaf venation etc. are very significant in tracing the phylogeny. Again the study of anatomy regarding the type of xylem, nature of vessels and the development of stele among the members of pteridophytes, gymnosperms and angiosperms furnish additional support for the doctrine of evolution. The almost identical anatomy of stems of gymnosperms and angiosperms supports evolution of gymnosperms from angiosperms.

(4) *Evidence from Comparative Embryology*—The study of the comparative embryology (i.e. the nature and the development of the embryo from the one-celled zygote) in plants and animals gives

again some interesting evidences in favour of organic evolution. The development of the embryo from the zygote up to the formation of the young sporophyte exhibits a striking resemblance to certain forms from which they have been derived e.g. in one Australian species of *Acacia*, the seedlings have compound leaves like its ancestors i.e. like other species of *Acacia* but the adult Australian *Acacia* is characterised by simple leaves with phyllodes. Adult cactus plants have no typical leaves at all, although leaves may be represented by spines; but the seedlings of cactus have readily recognisable leaves. In the life history of moss plant, spore on germination gives rise to a filamentous alga-like structure (protonema); fern spore on germination gives rise to a filamentous alga-like structure from which a thalloid prothallus resembling a liverwort develops —from this thalloid prothallus, mature fern plant develops. All

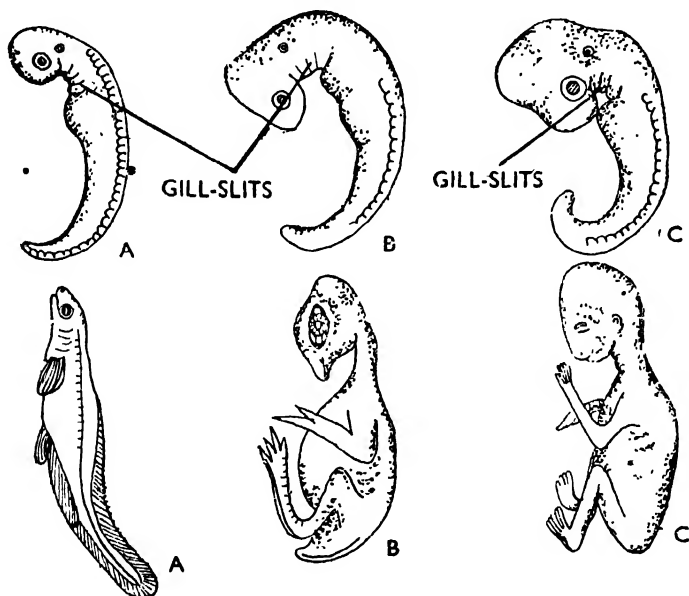


Fig. 2.1 Diagram showing the early (upper row) and late (lower row) stages of the development of the embryos of different vertebrates.
A—Fish, B—Chick and C—Human

these support the facts that at the time of the development, some of the ancestral characters are being repeated by the plants in their early stage of development. From these observations, Haeckel established his *theory of recapitulation* or *biogenetic law* according to which “ontogeny recapitulates phylogeny”—in other words “the different stages in the development of an individual (ontogeny) represent the different stages through which the race passed (phylogeny) in the process of evolution.” Again the origin of one plant group from another plant group may be traced from the study of the

embryology e.g. *Gnetum*, a gymnosperm, resembles angiosperms embryologically in many respects i.e. in the formation of tetrasporic-female gametophyte, reduced male gametophyte, the development of embryo by lying down a transverse wall in the zygote cell etc.—hence it is assumed that angiosperms had their origin from gymnospermous ancestor like *Gnetum*. Jeffrey has observed an interesting and possibly comparable phenomenon in conifers. If conifers are injured and the wound allowed to heal, the new growth may differ histologically from normal tissue ; in such instances, the new tissue shows a type of structure which is well known from fossil conifers of the mesozoic era.

Further, the figure 2.1 illustrates the fact that the young developing embryos of different vertebrates show a great similarity to one another. In all the cases, including human embryo, tail and gill slits are found to be present at one stage of the development—this condition leads scientists to confirm the theory of recapitulation.

(5) *Evidence from Comparative Physiology*—Study of comparative physiology and biochemistry, though not much bears, still provides some of the evidences for evolution. As some of the by-products of metabolism and physiological processes are common in certain groups of plants so they show origin from common ancestor. For example, the enzymes produced by plants are in the main similar ; the chemical reactions involved in the mechanism of respiration are essentially similar in most of the different groups of plants ; the process of photosynthesis carried out by all green plants ranging from thallophytes to spermatophytes are similar. Again, the serodiagnostic tests of the members of the families of angiosperms help greatly in tracing out the phylogeny among themselves.

(6) *Evidence from Geographical Distribution*—Geographical distribution of plants and animals also supplies some evidence in support of organic evolution. In lands situated near each other, the flora is more or less similar in comparison with remotely situated lands e.g. the flora of the plains of Bengal and Bihar are very much alike but differ from those of the hills of South India, Punjab or of the deserts of Rajasthan. Sometimes in the same tract of country, the occurrence of some of the genera of remote land with the local flora side by side indicates their origin from common ancestor. Sometimes some species are found to confine to a particular area due to some barriers like lofty mountain, deserts and seas. These barriers are responsible for the origin of isolated i.e. endemic species of a particular area. Again endemic species are often found to originate with some closely allied species—this shows that all the allied species have originated from the same ancestor.

(7) *Evidence from Domestication*—By domestication of plants and animals, variations in offspring and the origin of new varieties may take place. Domestication of plants means the culture or cultivation of plants. Plants have been cultivated by man since pre-historic times. They have produced new varieties of plants by various agricultural and horticultural methods such as hybridization,

layering, grafting, cuttings etc. These methods throw some light in support of organic evolution, e.g. the origin of present-day rose from wild rose of earlier type, the origin of all cultivated forms of *Brassica* (i.e. the different varieties of *Brassica*) from the wild type (*Brassica oleracea*), origin of tetraploid american cotton from an old world cotton species having 26 chromosomes through crossing, origin of *Raphanobrassica* (a tetraploid new species) by crossing wild cabbage (*Brassica oleracea*, $2n$) and radish (*Raphanus sativus*, $2n$) etc.

(8) *Evidence from the facts of Mutation*—Sometimes some individual plants are found to vary greatly from the parent species and as a result of such change, they form new species. These natural variants are called *mutants* and the phenomenon of this change is called *mutation*. Origin of mutants strongly supports the theory of evolution.

Theories of Organic Evolution

After the acceptance of the doctrine of descent, a question arose among biologists as to the methods and causes of evolution. To answer this question i.e. how evolution has taken place, several theories have been put forward from time to time. Most of the earlier theories were based on speculations rather than facts—those speculative theories on the origin and evolution of life have already been discussed in the introductory chapter. During the nineteenth and early twentieth centuries some great theories to explain the cause, course and effect of organic evolution were proposed by Lamarck, Charles Darwin, de Vries, Weismann and others.

3.1 Lamarck's Theory i.e. Lamarckism : Jean-Baptiste Pierre Antoine de Monet Lamarck (1744-1829), a French biologist, postulated the first modern theory to explain the cause of evolution in 1802 in his book '*Philosophie Zoologique*'. Lamarck began his career as a botanist, but became a zoologist when he was offered an appointment in Zoology Department at the Jardin des Plantes. Lamarck proposed a theory that characteristics acquired by organisms in response to changed conditions of life can be inherited by their offspring. According to him environment plays the main part in the evolution of living organisms. He observed in many cases that individuals of the same species growing under different conditions showed marked differences. This environmental change again leads to changes in the needs and wants of the organisms. In case of animals, the changed needs are met by a change in activities which involve the greater use of some organs and disuse of other organs. The use or exercise of organs or parts results in the formation of new organs while disuse or want of exercise results in degeneration of organs. According to him, the new characters thus acquired in each generation under such conditions are preserved and transferred to the offspring. The chief features of Lamarck's theory to explain the evolution of species may be discussed as follows :—

1. *The Direct Effect of the Environment*—Lamarck believed that change of form of either plants or animals was due to change in environment e.g., plants grown in the shade develop larger leaves and long internodes while the same plant grown under light will have smaller leaves and short internodes. Again, plants grown in dry soil have more elaborate root system than plants grown in wet soils. In the same plant, due to different environmental condition, heterophylly is observed. If mesophytic plants are brought accidentally in a desert and if they survive, xerophytic characters such as thick cuticle, sunken stomata, reduced leaf surface, stunted growth,

deeply penetrating tap root system etc. are produced. In case of plants, according to Lamarck, the effect of the environment is direct while in case of animals, the effect is indirect as the habits of animals are changed in the new environment and this change of habits causes the change of structure or form. From the above facts, Lamarck concluded that plants and animals react to environmental conditions and that as a result of cumulative effects produced by such changed conditions through generation after generation, new species may be evolved.

2. *Conscious Efforts*—Lamarck had the idea that organs of plants and animals are developed according to their urgent need. In other words, the 'need' of an organ causes an organ to develop. Thus the necessity or need of the development of spines, prickles, hairs etc. by plants as defensive organs would cause the growth of such organs.

3. *Use and Disuse*—Constant use or exercise of organs result in the formation of new organs or increase in size while disuse or want of exercise results in degeneration or disappearance in course of time. For example, some animals that live in great depths of sea where light can not penetrate, have very malformed eyes; according to Lamarck, the ancestors of such animals had well-formed eyes which degenerated due to disuse generations after generations. The horse-like ancestors of giraffe were forced to live in an area where there were only trees and no grass and other herbaceous vegetation. Hence, they had to feed on the leaves of trees and for this they had to stretch their neck in search of food from all trees—this 'use' resulted in the lengthening of the neck of giraffe.

4. *Inheritance of Acquired Characters*—All such habits and characters gained by living organisms during their life-time are transmitted to their offspring in the next generation and so on (for details refer article 3.5).

CRITICISM—Lamarckism could not explain the following points e.g. "(1) many characters of active adaptations, even though of simple kind, for example, the penetration of the lung-sacs of birds through hair-fine holes into all the bones; (2) many complicated adaptations of active organs: examples, flight-making organs, eyes, smelling organs, auditory organs; (3) all complicated passive adaptations: example, mimicry", hence Lamarck's theory is not at all sufficient to account for the origin of species. Moreover, now-a-days geneticists are of opinion that acquired characters are not inherited, hence Lamarck's position as an evolutionist is still uncertain.

3.2 **Darwin's Theory i.e. Darwinism**: Next theory to explain the evolution of living organisms was put forward by an English naturalist Charles Robert Darwin (1809-1882) in his classical book '*Origin of Species by means of Natural Selection or the Preservation of Favoured Races in the Struggle for life*' (1859). In that book he propounded the theory that organisms tend to produce offspring varying slightly from their parents, that the process of natural selection tends to favour the survival of those best adapted to their

environment and that by the operation of these factors new species may arise widely differing from each other and also from their common ancestors. Darwin's theory, based on natural observations and continuous experiments, is still one of the most widely accepted theories that attracted the scientific world to believe in the doctrine of evolution. His theory is popularly known as 'the theory of natural selection' and is based on several important factors which are as follows :—

1. *Overproduction* i.e. *Prodigality of Production*—The living beings both plants and animals produce in nature more offsprings than could ordinarily survive. This overproduction of offsprings prevents a race of plants and animals from extinction. It has been noted that plants and animals tend to multiply at high geometrical rates e.g. *Capsella bursa-pastoris* (Cruciferae) produces more than 50,000 seeds ; *Nicotiana tabacum* (Solanaceae) produces about 360,000 seeds annually, although all the seeds neither mature nor germinate to give rise to offsprings, still the number of offsprings that reaches maturity is enough to maintain the species.

2. *Struggle for Existence*—Overproduction causes a continuous struggle amongst living organisms for food, space, light, water and other environmental factors. If all the seeds of a particular plant were to germinate and develop into mature plants, then a vast area on the earth would be covered by them. If, in this way, all the seeds of all the plants were to germinate and develop into mature plants then a keen competition, called struggle for existence, will be set up among themselves for food, space, light etc. According to Darwin the struggle for existence is either *intraspecific* i.e. between different plants and animals of the same species or *interspecific* i.e. between plants and animals of different species, or *environmental struggle* between the living organisms and the physical environment like flood, volcanic eruption, earthquake etc. Those who can adapt themselves as a result of such struggle are called *victors* and those who are unable to adapt are called *unfit* or *vanquished*. The victors can only survive and the unfit perish or become extinct.

3. *Variation*—Offspring of either plants and animals do not resemble each other exactly and absolutely ; there are always, even slight variations between them. Darwin suggested that these variations are preserved and transmitted to the offsprings. Such variations help the individuals in the environmental struggle for existence or may not help, rather may be a drawback. Hence some are more suitably fitted for the struggle while others are ill-fitted.

4. *Natural Selection* or *Survival of the Fittest*—This is the principal mechanism of evolutionary change. In the struggle for existence only the individuals having favourable variations survive, eliminating others (with unfavourable variations) which are not well-fitted. In other words, the individuals best adapted to the natural conditions will survive while others which are unable to adapt will perish. This condition of the survival of the fitted individuals led

Darwin to call 'survival of the fittest.' Darwin called "survival of the fittest" *natural selection* as "survival of the fittest" is a type of selection exercised by nature—during selection, nature has selected only the fittest one and consequently eliminated all the unfit.

5. *Heredity and Origin of Species*—In the struggle for existence, when the victors survive, the characters of the survived variants are passed to their offsprings in the next generations. So the variation that caused the fit-ones to survive becomes a part of the character. Darwin believed that these minute variations of fluctuating types piled up generations after generations. Ultimately, these slight variations were accumulated through several generations and thus produced some important modified structure which led to the origin of new species out of old types.

CRITICISM—Though the phenomenon of natural selection is one of the very important and pioneer factors to explain the cause of evolution, yet Darwinism has not been accepted universally due to following drawbacks :—

(a) Darwinism accounts for the survival of the fittest but not the arrival of the fittest.

(b) It is accepted that by natural selection some organisms survived, while others perished. Darwinism only states the effect of this natural selection but not the causes of degeneracy.

(c) Darwinism only explains the struggle amongst young individuals but does not explain its influence upon adult characteristics.

(d) Natural selection is not always beneficial, as over-specialisation amongst the organisms due to natural selection leads to destruction.

(e) This theory did not take into sufficient account of the destruction of whole races of organisms irrespective of their fitness by natural calamities—in this respect we find also the survival of the weakest.

(f) Natural selection is unable to explain the existence of some structures present in plants and animals which are not helpful in their survival.

(g) Variations, that occur at random, can never be of the utmost importance and can not explain the production of highly organised and specialised structures.

A. **MODERN CONCEPT OF DARWINISM** i.e. **Neo-Darwinism** : The natural selection as formulated by Charles Darwin in his 'Origin of Species' could not satisfactorily explain the origin of new species. His theory established the fact of evolution but due to the lack of large mass of evidence there was a serious gap. Darwin's idea was that evolution was due to the natural selection of variations but he unfortunately could not explain how these variations arose. Since then, the mutation theory and other findings from genetics, systematics, ecology, morphology etc. have accumulated and a theory

acceptable to most of the modern evolutionists has been derived from Darwin's theory—this is known as *neo-Darwinism*. Neo-Darwinism may be stated simply as the revised view of Darwinism which includes the combination of ideas of Darwin, de Vries, Huxley, Fisher, Haldane, Muller, Dobzhansky and other modern biologists. Neo-Darwinism fundamentally differs from Darwin's original theory. Dobzhansky calls neo-Darwinism as biological theory of evolution because this theory is the result of synthesis of the findings of genetics, cytology, systematics, ecology, palaeontology, comparative anatomy, morphology etc. According to this theory "evolution is a result of mutation (genetic changes), with the recombination of genes through biparental reproduction under the influence of natural selection over long periods of time."

The main features of neo-Darwinism to explain the origin of new species are as follows :—

Different types of variation or variability occurring within a species are not uniformly distributed in the entire population of a species, rather somewhat restricted to a local population. Such population having a distinctive type of variable character is given the rank of a sub-species which again is considered as an incipient species. This incipient species i.e. sub-species ultimately becomes converted into a species through natural selection.

In each sub-species, there is a complex of gene-determined characters and these various genes in a complex are derived more or less from the same ancestors by mutation. The genes of a particular sub-species are not specific to it but are present in varying degree in different sub-species. Within each sub-species, a particular combination of genes is present—natural selection operates on this gene combination and ultimately these combinations are screened out by ecological factors. Then random mutation takes place within each sub-species, as a result different alleles arise in different sub-species. These sub-species are geographically isolated from each other, sometimes they may also be physiologically and ecologically isolated. Next, new mutations appear in an isolated sub-species which (i.e. mutation) can not be distributed uniformly within the entire population of a species. In this way, new species are ultimately formed by gradual mutation. According to neo-Darwinism, very small mutations serve as the raw materials of evolution; large mutations are generally disadvantageous, hence can not serve as raw materials.

3.3 Weismann's Theory : August Weismann (1834—1914), a German biologist proposed the theory of heredity, which assumes the continuity of the germplasm and the non-transmission of acquired characteristics. Hence he did not accept nor support the inheritance of acquired characters as postulated by Lamarck. He also observed that the "Theory of Natural Selection" does not explain the causes of degeneration of organs. Immediately after the death of Darwin, Weismann gradually developed his ideas of heredity from his observations regarding the variations in plants and animals. According

to him variations are of two types viz. (a) *congenital* i.e. organisms are born with them and (b) *acquired* during the life-time of a particular living organism. For the latter type of variation, Weismann was very much worried and he gradually postulated in his '*Germplasm Theory*' that acquired characters could not be inherited.

Weismann in his '*Germplasm Theory*' explained that living organisms consists of two kinds of materials viz. *germplasm* and *somatoplasm*. Somatoplasm produces only body cells while germplasm produces reproductive cells, the latter remains separated and secluded from the cells of the main body of the organism developing out of the germplasm. Germplasm, through reproduction, gives rise to offspring in which again germplasm develops and remains secluded from the somatoplasm. So germplasm is continuous generations after generations, the somatoplasm is discontinuous and is developed anew at every generation. As somatoplasm is discontinuous any change in it can not be transmitted in the next generation to the offspring. The germplasm is not influenced by any change in the somatoplasm. So Weismann explains that acquired characters which include changes during the life-time of an organism are not inherited by the offspring in the next generation; for example, a lame man's son does not turn out lame, the lameness acquired by the individual (i.e. change in the somatoplasm) is not transmitted to the offspring.

Further, Weismann advanced his theory regarding heredity which he thinks is influenced by certain *determiners* which are located within certain complicated bodies called *ids*, which make up the structure of chromosome. So long as these determiners remain unchanged the heredity of an organism does not change. In the beginning Weismann faced some difficulties to explain his theory of germplasm. But later he explained all such difficulties in his supplementary theories. Firstly, Weismann in his "hypothesis of parallel modification of germplasm and soma" explained that some variations of the soma (i.e. body) of the organism also involves a parallel variation of the germplasm—this variation is inherited. Secondly, he observed some *polymorphism* among plants and animals e.g. the development of two types of leaves within the same species in different ecological conditions i.e. the same species exhibits dissected leaves when grown in water and again entire leaves when grown on land; the same species of butterfly show different forms according to environment, nutrition etc. To explain this polymorphism, Weismann postulated '*germinal selection hypothesis*'. In this hypothesis he explained that germplasm has got different sets of determiners instead of a single set of determiner. It is the environment that decides which set of determiners will act to bring about the change. According to him, several sets of determiners struggle for expression within the germplasm but finally nature selects only one set of determiner for its expression.

CRITICISM : Weismann's theories of germplasm and chromosome heredity were highly appreciated by later workers—these

theories form the basis of genetics to explain the modern conception of inheritance through chromosomes. But his last supplementary theory could not explain the cause of evolution as that was based merely on speculation.

3.4 Mutation Theory of de Vries : Hugo de Vries (1848-1935), a Dutch botanist put forward a new theory in 1901 to explain the origin of new races and species. Previously, Darwin considered that only the minute fluctuating types or the continuous variations were important in evolution. According to him large, discontinuous variations i.e. sprouts were of no significance in evolution, de Vries in his 'Theory of Mutation' held that Darwin's fluctuating or continuous variations are not inheritable, rather large variations (sprouts) appearing suddenly and spontaneously in the offspring are the cause of evolution. de Vries called these sudden and discontinuous i.e. large variations '*mutations*'. According to de Vries, mutation causes a permanent change in the nature of the germ cells, while change in the soma and also germplasm, as a result of fluctuation is temporary and due to the effect of the environment. de Vries suggested that the permanent change in the germplasm only arises spontaneously out of the internal conditions ; out of these changes, some which are not adaptive perish and the only adaptive mutations 'survive'. He is of opinion that only sudden and large mutations play an important role in evolution while small mutations have no importance. New species appear suddenly from the parent species in a single step without showing any transitional forms. So the evolution is mainly due to internal causes but its course is controlled by the environment. Environment will select finally the survival of the mutants. de Vries based his mutation theory from the following experiments and observations :—

1. *The occurrence of elementary species*—de Vries gave the name elementary species to some varieties of both wild and domesticated plant species with *minute* differences that breed true.

2. *Mutation in evening primrose (Oenothera lamarckiana)*—*Oenothera lamarckiana* (Onagraceae) is a biennial cultivated garden plant with bright yellow flowers. In 1886, de Vries found this plant growing in a wild condition in a potato field near Amsterdam in Holland ; he also observed along with normal plants some variants of this plant that looked different from the normal plant. He brought all those variants at home and on cultivation found seven new species that bred true—de Vries called these new types *mutants*. On further cultivation for several generations, he found mutants with several characters which he classified as follows :

- (a) *Progressive species*—Species with additional characters.
- (b) *Regressive species*—Species with loss of some characters.
- (c) *Degressive species*—i.e. species with weak structures which will become extinct ultimately.

(d) *Inconstant species*—This group includes plants which did not breed true but produced mutants like the parent (*Oenothera lamarckiana*).

de Vries from his above experiments concluded that (1) mutations occur in all directions ; (2) the sudden appearance of new elementary species that attain immediately full constancy ; (3) the same mutants (i.e. new species) are produced again and again in large numbers which are usually subjected to natural selection and (4) the mutations are entirely different from fluctuating variations.

CRITICISM : The theory postulated by de Vries forms one of the most important modern theories to explain the cause of evolution but still there are some drawbacks in this theory as the material on which his work was based was found afterwards to be abnormal. de Vries found that *Oenothera lamarckiana* was an 'inconstant species' i.e. species without constancy (subjected to variation). The cause of this inconstancy of *O. lamarckiana* has been found out cytologically. *O. lamarckiana* is a structural hybrid or a complex heterozygous unstable species which never shows any chromosomal mutations. Most of the mutants obtained by de Vries were not mutants in the sense of gene mutation—they were rather the cases of mere unstable chromosomal aberrations. Hence de Vries' theory was based on the experiments with abnormal species—but still this theory holds good for the basis of the modern concept of evolution.

3.5 The Inheritance of Acquired Characters : It is a very problematic question and also a matter of discussion from the stand point of Lamarckism whether transmission of acquired characters to the offspring takes place or not. Acquired characters are the variations that are acquired by an organism during its life-time and the transmission of such characters i.e. variations to offsprings are the inheritance of acquired characters.

According to Lamarck, characters acquired by an individual during its own life-time are transmitted to the offsprings. Lamarck's theory of inheritance of acquired characters was not based on experiments. But random experiments performed by geneticists have disproved Lamarck's ideas which are discussed as follows :—

It has been proved that parts of the body having mutilation (i.e. by depriving part or making injury) are not inherited. For example, lame man's son does not turn out lame ; the battle injury on the bodies of soldiers do not beget crippled children ; Weismann's experiments by cutting of the tails of mice through successive generations did not give rise to offsprings without tails.

Sometimes cases of some congenital diseases like syphilis, tuberculosis etc. are quoted wrongly as hereditary. It has been proved that infection of those diseases may spread through the gametes or the embryo at some stage of its development in the womb. Hence, in true scientific sense such diseases are not the cases of inheritance.

Instinct is another factor by means of which most of the animals perform their activities in life. According to the concept of neo-Lamarckism, instincts are the "inheritance of the experiences of the previous generations" and therefore hereditary. But neo-Darwinism explained this in another way—according to this theory instinct is not hereditary, it develops in animals at particular stage of development when they behave in that way. For example, the instinct of birds to build their nests only develops at a particular stage when they are able to do that.

The inheritance of the effect of environment on the form and structure of plants and animals is another important point of discussion among geneticists. It has been found that many different forms of plants and animals of the same type grow in different environmental conditions. Now question arises how did these different forms came in? Supporters of neo-Lamarckism (i.e. neo-Lamarckians) are of opinion that those forms are the causes of variations acquired only in response to the environment. Another example of neo-Lamarckism is the effect of light on the skin colour. People having darker skin live near the equator where the light is strong but the people of the northern latitudes are fair-skinned due to the effect of weak light intensity. Exposure to sunlight causes darkening of the skin of fair human beings compared to less exposed human. Neo-Lamarckians think that dark colour of the tropical people is an acquired character. If this acquired character was inherited, the offspring of the darker parents would tend, even slightly, to be darker than offspring of fair parents when offsprings of both groups are reared in equal sunlight.

Some more experiments cited by neo-Lamarckians may be mentioned to explain the question of inheritance of acquired characters. Kammerer's work, although not verified by later workers, support the theory of inheritance of acquired characters. He carried out experiments with two species of salamander e.g. *Salamander atra* (a terrestrial alpine species that produces normally two offsprings at a time) and *S. masculosa* (an amphibious type producing many offsprings at a time)—when the former species was subjected to tropical moist climate, it produced more than two offsprings. Similarly, when *S. masculosa* was subjected to terrestrial and alpine conditions, it produced only 2 or 3 young ones which became terrestrial having vestigial gills only. The action of the environment on evolution may be cited in case of the change in the peppered moth types. In England, the normal type having light mottled wings (which was once the prevalent type in agricultural England) often produced black melanic type mutants—this black melanic type now-a-days has well adapted, for camouflage, the sooty atmosphere of the modern industrial England.

The question of inheritance of acquired characters is still a debatable one among the geneticists although numerous experiments have been carried out to prove the theory. But modern geneticists believe

that acquired characters can not be inherited as such, hence the evolution of new species is not possible through inheritance of acquired characters. The only possible way to explain the cause of evolution of new species is the selection of mutations or hybrid phenotypes.

SELECTED QUESTIONS

1. What do you mean by the term organic evolution ? Give a brief account of the earlier views regarding the concept of organic evolution.
Refer chapter 1 (paras 3, 8-14).
2. Give an account of the principles on which Charles Darwin proposed the theory of organic evolution.
Refer article 3.2 (excluding A.)
3. Give a brief account of what you know of the Mutation Theory of de Vries and discuss its importance in explaining organic evolution.
Refer article 3.4
4. Give an account of the theory of evolution as suggested by Darwin and bring out its difference from that of Lamarck.
Refer articles 3.2 and 3.1
5. In the light of present day knowledge discuss the role of Natural Selection as a factor in evolution.
Refer article 3.2 (including A.)
6. Bring out the fundamental differences between the different theories of evolution as suggested by de Vries, Lamarck and Darwin.
Refer articles 3.1, 3.2 and 3.4
7. Discuss whether acquired characters are inherited.
Refer article 3.5
8. Discuss in brief the evidences in support of organic evolution.
Refer chapter 2
9. Briefly describe the contribution of the following scientists—
 - (a) Hugo de Vries—Refer article 3.4 (Para one).
 - (b) Lamarck—Refer article 3.1 (Para one).
 - (c) Weismann—Refer article 3.3 (Para one).
 - (d) Charles Darwin—Refer article 3.2
10. Write short notes on :—
 - (a) Struggle for existence—Refer article 3.2,, 2
 - (b) Inheritance of acquired character—Refer article 3.1, 4
 - (c) Natural Selection—Refer article 3.2, 4

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